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SICULOSCIADIUM, A NEW MONOTYPIC GENUS OF APIACEAE FROM SICILY[1]

Cristian Brullo,[2] *Salvatore Brullo,*[2] *Stephen R. Downie,*[3] *Clark A. Danderson,*[3] *and Gianpietro Giusso del Galdo*[2]

ABSTRACT

The results of a morphological and molecular systematic investigation of the poorly known Sicilian endemic species *Peucedanum nebrodense* (Guss.) Nyman (Apiaceae subfam. Apioideae) are presented in order to better characterize the species and clarify its phylogenetic position. Morphological, karyological, anatomical, and ontogenetic studies indicate that this species is taxonomically distinct. Phylogenetic analysis of combined morphological and nuclear ribosomal DNA (nrDNA) ITS sequence data suggests an affinity with *Dichoropetalum* Fenzl, whereas an unweighted pair group method with arithmetic mean (UPGMA) analysis, based on 36 morphological characters, suggests that *P. nebrodense* is similar to *Ormosolenia* Tausch. Given its unusual life cycle; distinct suffruticose, evergreen, and dwarf habit; and peculiar fruit anatomy, we recognize *P. nebrodense* as distinct from *Ormosolenia* and *Dichoropetalum*, and we treat it as the new monotypic genus *Siculosciadium* C. Brullo, Brullo, S. R. Downie & Giusso based on *S. nebrodense* (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso [≡ *Pteroselinum nebrodense* Guss.], which is lectotypified herein.

Key words: Apiaceae, IUCN Red List, *Peucedanum*, Sicily, *Siculosciadium*.

The genus *Peucedanum* L., as traditionally defined within the Apiaceae, contains more than 100 species of Eurasian and African distribution (Pimenov & Leonov, 1993). However, the genus has long been regarded as an unnatural group, and the need for its reduction into smaller, monophyletic units has been proposed by many (Pimenov, 1987, 1992; Burtt, 1991; Pimenov & Leonov, 1993; Ostroumova & Pimenov, 1997; Reduron et al., 1997; Shneyer et al., 2003; Pimenov et al., 2007). Indeed, the subdivision of the large polymorphic genus *Peucedanum* into natural groups is "among the most urgent challenges" facing the realization of a modern classification of the family Apiaceae (Winter et al., 2008: 347). The results of molecular systematic investigations have confirmed the polyphyletic nature of *Peucedanum* s.l., and, as a consequence, the genus is now reduced to only a few species allied to the type species, *P. officinale* L., and several segregates of *Peucedanum* are now recognized as distinct genera (Downie et al., 1998, 2000; Spalik et al., 2004; Winter et al., 2008; Magee et al., 2009). The results of these investigations also placed *Peucedanum* s. str. and other segregates in the revised Apiaceae tribe Selineae (Spalik et al., 2004; Downie et al., 2010).

[1] The authors thank the curators of the herbaria cited in the text for the loan of herbarium materials. We are also very grateful to M. C. Terrasi for help with the karyological investigations and to G. Venora for help with the fruit anatomy.

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One species of *Peucedanum* whose biology and phylogenetic placement have yet to be investigated is *P. nebrodense* (Guss.) Nyman. This species was first referred to *Imperatoria chabraei* Spreng. by Gussone (1827), based on specimens from the Madonie Massif (northern Sicily), which still represents its sole locality. Gussone (1844) later attributed the population from Madonie to a new species, namely *Pteroselinum nebrodense* Guss., and highlighted its morphological differences from *Pteroselinum chabraei* (Spreng.) Rchb. Nyman (1855) later ascribed this species to the genus *Peucedanum*, a transfer supported by both Cesati et al. (1884) and Strobl (1886). Subsequently, Paoletti (1900) and Fiori (1925) considered this taxon a variety of *Peucedanum carvifolia* (L.) Vill. Pignatti (1982), however, stressed the unclear and still unsolved taxonomic position of *P. nebrodense*, and Banfi et al. (2005) attributed this species to the genus *Holandrea* Reduron, Charpin & Pimenov, although without substantiating evidence. It is likely that the classification proposed by Banfi et al. (2005) was based on the transfer of *Peucedanum carvifolia* into the genus *Holandrea* by Reduron et al. (1997).

Because of their rarity and extreme localized distribution, specimens of *Peucedanum nebrodense* are not commonly found in major European herbaria, and the species is usually not treated in European floras. The plant does have a very unusual habit, however, when compared with the other known species of *Peucedanum*, which are commonly hemicryptophytes. *Peucedanum nebrodense* is characterized by a dwarf shrubby habit with many woody branches and persistent leaves. As such, the species appears taxonomically well isolated, showing a morphological affinity only with *P. alpinum* (Sieb. ex Schult.) B. L. Burtt & P. H. Davis from Crete, a taxon recently attributed by Pimenov (1992) to the restored genus *Ormosolenia* Tausch. The morphological similarities between these species include their branched rootstocks, well-developed caudices, and polycarpic life form. To better characterize the poorly known species *P. nebrodense* and to address its taxonomic position, we conducted morphological, karyological, and anatomical studies, and present herein the results of a phylogenetic analysis of this species and its closest allies, using morphological and molecular evidence.

Materials and Methods

GENERAL MORPHOLOGY

Morphological investigations of *Peucedanum nebrodense* were based on an examination of living material collected from the type locality. In order to understand its ontogeny and phenology, fruits, seedlings, and mature plants were cultivated at the Botanical Garden of Catania, Italy, for several years. Additional characters considered were those of leaves and other vegetative organs, inflorescences, flowers, and fruits. Specimens of *P. nebrodense* were examined from herbaria B, CAT, FI, G, M, NAP, PAL, RO, W, and WU. Specimens from *Dichoropetalum* Fenzl, *Johrenia* DC., *Ormosolenia*, *Peucedanum* s. str., and *Zeravschania* Korovin were also included in this comparative examination of general morphology, with emphasis placed on *P. nebrodense* and *Ormosolenia*. Recently, Pimenov et al. (2007) considered *Holandrea*, *Johreniopsis* Pimenov, and some species of *Johrenia* and *Peucedanum* as belonging to the genus *Dichoropetalum*.

KARYOLOGY

Mitotic metaphase plates were obtained from squashed root tips of cultivated plants of *Peucedanum nebrodense*, pretreated with 0.3% colchicine water solution for three hours and fixed in ethanol-acetic acid (3:1) for six hours, then hydrolyzed in 1N HCl for seven minutes and stained, according to the Feulgen method. Metaphase observations and chromosome measurements were made using the image analysis systems IKAROS 4.6 (Metasystem, Altlussheim, Germany) and Zeiss (Oberkochen, Germany) AxioVision 5.1. Karyotyping was done with the software Cromolab 1.1 (Brullo, 2002–2003), which was used to recognize homologues, to order chromosomes by size, and to classify them according to morphology and centromere position (Levan et al., 1964). Ten mitotic plates from five individuals were used to determine the karyotype.

ANATOMY

Fruit and leaf petiole anatomy was examined from living material collected from the type locality, fixed in Karpechenko solution, and then embedded in paraffin. Transverse sections were double stained with ruthenium red and light green. Comparisons in leaf petiole anatomy were made between *Peucedanum nebrodense* and a putative ally, *Ormosolenia alpina* (Sieber ex Schultes) Pimenov.

PHENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS

We supplemented and slightly modified the morphological data matrix provided by Pimenov et al. (2007) in their comparative multivariate analyses of *Holandrea*, *Johrenia*, *Johreniopsis*, *Peucedanum* s.l., and *Zeravschania* by including the species *Ormosolenia alpina*, *O. pisidica* Boiss. & Heldr., and *P.*

nebrodense and two additional characters (i.e., leaf persistence and rootstock habit). In total, the data matrix comprised 36 morphological characters (Appendix 1) and 41 species. The importance of these characters in distinguishing among these putatively related taxa has been highlighted by Pimenov et al. (2007). No data cells in the matrix were scored as missing. Our rationale for including a phenetic analysis in this paper was to comprehensively compare those diagnostic characters across all included taxa to ascertain what species might be most similar morphologically to *P. nebrodense*. The resultant data matrix is presented in Appendix 2. Cluster (unweighted pair group method with arithmetic mean [UPGMA]) analysis of these data was implemented by using the NTSYSpc package (Rohlf, 2000).

DNA SEQUENCING

Total genomic DNAs of *Ormosolenia alpina*, *O. pisidica*, and *Peucedanum nebrodense* were extracted from approximately 20 mg of dried leaf tissue using a DNeasy Plant Mini Kit (Qiagen, Valencia, California, U.S.A.). The nuclear ribosomal DNA (nrDNA) ITS region in each of these species was polymerase chain reaction (PCR)-amplified by using the protocol described in Downie and Katz-Downie (1996). For template purification, the QIAquick PCR Purification Kit (Qiagen) was used. Sequencing reactions were carried out using a BigDye Terminator Cycle Sequencing Kit (version 3.1; Applied Biosystems, Foster City, California, U.S.A.) and sequenced with an ABI 3730xl sequencer (Applied Biosystems). The simultaneous consideration of both DNA strands across the entire ITS region permitted unambiguous base determination. ITS sequence heterogeneity, as evidenced by polymorphisms at single bases in otherwise perfect chromatograms, was not detected for any accession. GenBank accession numbers and specimen voucher information for *O. alpina*, *O. pisidica*, and *P. nebrodense* are presented in Table 1.

PHYLOGENETIC ANALYSES OF MOLECULAR AND MORPHOLOGICAL DATA

To ascertain the phylogenetic positions of *Ormosolenia alpina*, *O. pisidica*, and *Peucedanum nebrodense*, their ITS sequences were first analyzed with 40 additional ITS sequences from other members of the Apiaceae, tribe Selineae. These sequences were obtained from GenBank and represented most major clades of the tribe. Included here were representatives of Eurasian *Peucedanum* and its segregates, including *P. officinale* (the type for *Peucedanum*), *Imperatoria* L., and *Pteroselinum* Rchb., and *Zeravschania* Korovin and *Pimpinella* L. (both in tribe Pimpinelleae) were used to root the trees. These sequence data were analyzed using maximum parsimony as implemented by PAUP* version 4.0b.10 (Swofford, 2003), and the resultant strict consensus tree revealed that *Ormosolenia* and *P. nebrodense* comprised a well-supported clade along with representatives of *Holandrea*, *Johrenia*, and *Johreniopsis* (many of which have been treated as species of *Dichoropetalum*, according to Pimenov et al., 2007). Sister group to this clade was *Aethusa cynapium* L. Subsequently, another data matrix was produced to include all species of *Holandrea*, *Johrenia*, and *Johreniopsis* for which ITS data were available in GenBank. Thirteen species comprised this matrix, including *Ormosolenia* and *P. nebrodense*, and *A. cynapium* was used to root the resulting phylogenetic trees. GenBank accession numbers and voucher information for these species are presented in Table 1. This reduced matrix was analyzed by using heuristic maximum parsimony searches and 1000 replicate analyses, random stepwise addition of taxa, and tree bisection-reconnection (TBR) branch swapping. Bootstrap values were calculated from 1000 replicate analyses, using TBR branch swapping and simple stepwise addition of taxa. In the phylogenetic analysis of morphological data, 17 parsimony-informative morphological characters were considered, representing both vegetative and reproductive structures (Appendix 3). Eleven characters were binary, the remaining multistate; all characters were unordered and equally weighted. The taxa included in this portion of the study corresponded to those included in the 13-species ITS matrix, and the data matrix of morphological characters is presented in Appendix 4. These ITS and morphological data were analyzed separately and combined, with only the results of the combined analysis presented herein. Separate maximum parsimony analysis of each data set resulted in highly consistent yet generally poorly resolved and weakly supported trees, whereas analysis of the combined matrix yielded trees of greatest resolution and highest branch support overall. The data matrix of combined morphological and ITS sequence data, as well as the resulting strict consensus tree, is available from TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S12922>).

Results and Discussion

KARYOLOGY

According to Solov'eva et al. (1985) and Pimenov et al. (2003), species of *Peucedanum* s.l. are usually

Table 1. Accessions of Apiaceae examined for nuclear ribosomal DNA ITS sequence variation, with specimen voucher information and GenBank accession numbers. Two GenBank accession numbers for a taxon refer to ITS-1 and ITS-2 data only, with no data available for the intervening 5.8S region; a single GenBank accession number indicates that 5.8S data were available and used in the phylogenetic analysis. With the exception of data for the two *Ormosolenia* species and *Siculosciadium nebrodense*, all ITS data were previously published by others and obtained from GenBank. Nomenclature follows Pimenov et al. (2007).

Taxon	Voucher information	GenBank accession number(s)
Aethusa cynapium L.	Germany. Cult. at UIUC from seeds, Univ. Oldenburg Bot. Gard., Germany, *Downie 127* (ILL)	GQ862376
Dichoropetalum achaicum (Halácsy) Pimenov & Kljuykov	Greece. N. Pelóponnisos, Vouraikos Gorge, *Southam s.n.* (E), cult. Royal Bot. Gard. Edinburgh (no. 19912669)	AF164832, AF164857
D. aromaticum (Rech. f.) Pimenov & Kljuykov	Iran. *Ajani s.n.* (Herb. Hossein Akhani, Univ. Tehran)	EU169288
D. carvifolia (Vill.) Pimenov & Kljuykov	France. Isère, mont Bovinant, Chartreuse, 22 Aug. 1989, *Reduron s.n.* (WA)	AF495828, AF495829
D. golestanicum (Rech. f.) Pimenov & Kljuykov	Iran. *Ajani 2053* (TEH)	EU169289
D. paucijugum (DC.) Pimenov & Kljuykov	Iran. *Ajani 852* (Herb. Hossein Akhani, Univ. Tehran)	EU169290
D. pschawicum (Boiss.) Pimenov & Kljuykov	Russia. S. Ossetia, Bad, *Pimenov et al. 112* (MW), cult. Moscow State Univ. Bot. Gard.	AF008619, AF009098
D. schottii (Besser ex DC.) Pimenov & Kljuykov	France. Alpes-Maritimes, col de Brouis, 30 July 1981, *Reduron s.n.* (WA)	AF495830, AF495831
D. scoparium (Boiss.) Pimenov & Kljuykov	Iran. Arak Prov., Zalion Pass betw. Arak & Borujet, 33°53′N, 49°00′E, 17 June 2001, *Pimenov et al. 406* (MW)	AY941274, AY941302
D. seseloides (C. A. Mey.) Pimenov & Kljuykov	Iran. Tehran Prov., *Ajani 2057* (TEH)	EU169291
Ormosolenia alpina (Sieber ex Schult.) Pimenov	Greece. Crete, Lefka Ori, Mt. Pachnes, 1 Sep. 2006, *Brullo & Giusso del Galdo 2061* (CAT)	HQ269391
O. pisidica Boiss. & Heldr.	Turkey. Davraz Dag, 20 June 1998, *Brullo & Pavone s.n.* (CAT)	HQ269392
Siculosciadium nebrodense (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso	Italy. Sicily, Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 24 July 2002, *Brullo & Giusso del Galdo s.n.* (CAT)	HQ269390

diploid ($2n = 2x = 22$), a feature common in the subfamily Apioideae. *Peucedanum nebrodense* has a diploid chromosome count $2n = 22$ (Fig. 1A, part 1), as previously reported by Duro et al. (2003), and has a karyotype characterized by five metacentric pairs of chromosomes, by five pairs of chromosomes approximate to the submetacentric type, and by one subtelocentric pair (Fig. 1A, part 2). Two chromosome pairs have microsatellites. This karyotype differs from those of other examined *Peucedanum* species, including those species recently transferred to *Dichoropetalum* (i.e., *D. carvifolia* and *D. pschawicum*), and from those of genera segregated from *Peucedanum* s.l. (i.e., *Imperatoria* and *Thysselinum* Adans.; Solov'eva et al., 1985). The karyotype of *Peucedanum* s.l. is characterized by at least seven pairs of metacentric chromosomes, while telocentric chromosomes have never been detected. Similarly, in *Peucedanum* s.l., microsatellites are absent or, if present, occur in one pair of chromosomes only. Karyological data are currently unavailable for other species of *Dichoropetalum* and *Johrenia*, as well as for *Ormosolenia* and many other Apiaceae. Nevertheless, the karyotype of *P. nebrodense* appears to be unique, bolstering its possible isolated taxonomic position within the Apiaceae.

LEAF MORPHOLOGY AND PETIOLE ANATOMY

Peucedanum nebrodense has 2-pinnate leaf blades, occasionally 1-pinnate in the cauline leaves, with sessile or subsessile leaflets (Fig. 1B, part 1). The basal leaves are always long-petiolate, although in the cauline ones the petiole tends to reduce progressively upward until disappearing; in such cases, the leaf blades are inserted directly on the sheaths. The petioles in cross section are falcate, with an adaxial groove, and have five collenchymatous ribs in the abaxial face and two in the adaxial face. Vascular bundles are five, all arranged in the peripheral part of the parenchyma, and interpose with four secretory

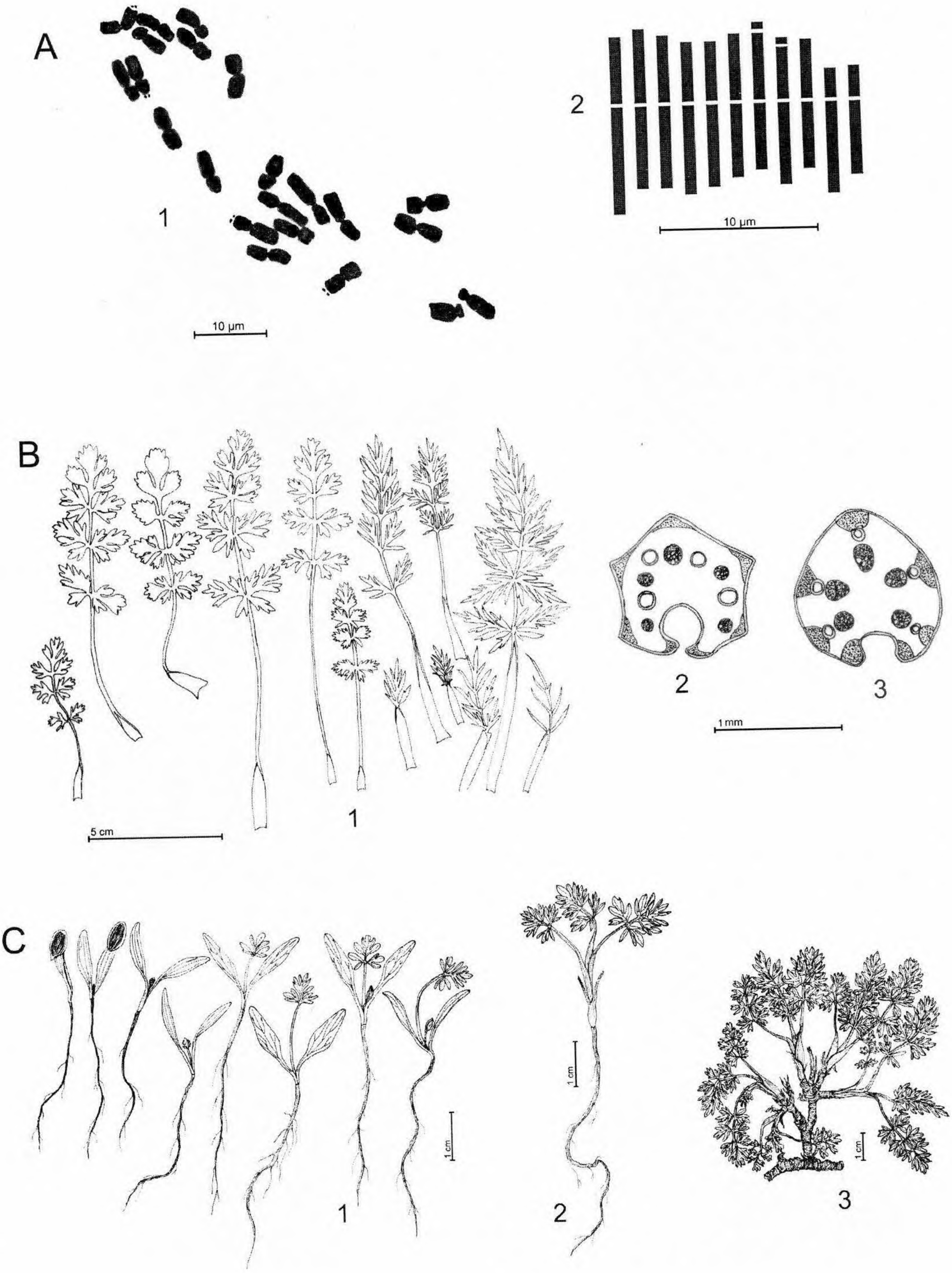


Figure 1. —A. Mitotic chromosome number of *Siculosciadium nebrodense*. —Part 1. Somatic metaphase plate. —Part 2. Karyotype ($2n = 22$). Root tip preparations from the 24 July 2002 collection, *S. Brullo, G. Giusso del Galdo & S. Sciandrello s.n.* (CAT). —B. Leaf variability of *S. nebrodense*. —Part 1. Living material from Madonie (Sicily). —Part 2. Petiole cross section of *S. nebrodense*. —Part 3. Petiole cross section of *Ormosolenia alpina*. —C. Vegetative stages of *S. nebrodense* (all living material taken from Madonie, Sicily). —Part 1. Seedlings. —Part 2. Juvenile plant. —Part 3. Adult sterile plant.

ducts (Fig. 1B, part 2). The petiole anatomy of *Ormosolenia alpina* is rather different from that of *P. nebrodense*. The petiole cross section of *O. alpina* shows that its collenchymatous ribs are not prominent (Fig. 1B, part 3). Interposed among the collenchymatous ribs and vascular bundles are five secretory ducts that unlike in *P. nebrodense* are directly in contact with the collenchyma. The leaf morphology of *P. nebrodense* suggests an affinity to some species of *Dichoropetalum* (Pimenov et al., 2007), whereas the petiole anatomy of *P. nebrodense* is unusual within the group.

FRUIT MORPHOLOGY AND ANATOMY

The mericarps of *Peucedanum nebrodense* are subrounded to elliptical, dorsally compressed, with distinctive spongy wings. The stylopodium is conical-flattened and the curved stylodium is much longer than the stylopodium (Fig. 2A, parts 1, 2). The exocarp is single-layered, interrupted near the ventral portion of the wings, and followed by an irregularly stratified parenchyma interspersed with thin-walled cells in the outer mesocarp and thickened in the ribs; the vascular bundles and secretory ducts are sunken in this parenchyma (Figs. 2B, 2C). The inner layer of the mesocarp consists of one row of tangentially elongated prosenchymatous cells with slightly lignified walls. The endocarp consists of one row of collenchymatous cells. Five of 11 oil ducts are associated with as many vascular bundles, four are vallecular and two are commissural, but do not reach the mericarp base. According to Pimenov (1992) and our own observations, the aforementioned features are quite different from those of *Ormosolenia alpina* and *O. pisidica* (Figs. 2A, parts 3–6; 2C, parts 2, 3). The latter two species are characterized by a more flattened stylopodium, a stylodium shorter than the stylopodium, three to six vittae per vallecula, and four to eight commissural vittae (secretory ducts associated with vascular bundles are not always present). The inner layer of the mesocarp of both species consists of three to five rows of elongated prosenchymatous cells and the single-layered endocarp also has tangentially elongated cells. The mericarp anatomy of *Dichoropetalum*, *Johrenia*, and *Zeravschania* is rather variable, but is always well differentiated from that of *P. nebrodense* (Pimenov et al., 2007). In summary, the peculiar fruit morphology and anatomy of *P. nebrodense* do not suggest any close taxonomic ally.

LIFE CYCLE

Both field and greenhouse observations reveal that *Peucedanum nebrodense* is characterized by a life cycle quite different from that known for other species of *Peucedanum* and *Ormosolenia*. The mericarps of *P. nebrodense* reach maturity between early September and October, when they gradually become loose and fall. These mericarps remain for about four months (December to early April) under the snow bed and only after the snow melts do they start to germinate (late April to May). The seedlings are characterized by well-developed roots, two oblanceolate to ovate-oblanceolate cotyledons that abruptly narrow into a 3-nerved petiole (0.5–0.8 mm), and a null hypocotyl (Fig. 1C, part 1). The blade is 8–13 × 1.5–4 mm, 3-nerved, with secondary nervation at maturity. The primordial leaf is 1- to 2-pinnate, long-petiolate, and subequal or longer than the cotyledons. Afterward, the seedling produces other leaves and, after this stage, it develops rhizomes bearing new leaves at its apex (Fig. 1C, part 2). During the second year, the rhizomes grow and branch, producing a well-developed rootstock (Fig. 1C, part 3). From June to early September, the caudices produce flowering stems from the center of the leaf rosette. Therefore, *P. nebrodense* is a perennial, polycarpic, and evergreen plant because its leaves persist through the winter (under the snow bed), a feature we observed on both wild and cultivated plants. *Peucedanum* s. str., *Dichoropetalum*, *Johrenia*, and *Zeravschania* are characterized by mono- or polycarpic plants with well-developed taproots, and basal leaves arranged in deciduous rosettes, usually with the remains of petioles at the stem base, while *Ormosolenia* is polycarpic with branched rootstocks, only basal leaves that are entire or 1-pinnate, with blades reniform to orbicular. *Peucedanum nebrodense* possesses an unusual life cycle and its suffruticose, evergreen, and dwarf habit is distinctive within the group.

PHENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS AND COMPARATIVE MORPHOLOGY

Peucedanum nebrodense has been considered morphologically similar to *P. carvifolia* (Paoletti, 1900; Fiori, 1925; Banfi et al., 2005), the latter recently included by Pimenov et al. (2007) in *Dichoropetalum* sect. *Holandrea*. In contrast, the unweighted pair group method with arithmetic mean (UPGMA) phenogram (Fig. 3A) revealed that *P. nebrodense* clustered with *Ormosolenia alpina* and *O. pisidica* and was separate from any species attributable to *Dichoropetalum* (including *Holandrea*), *Johrenia*, or *Zeravschania*. There are, however, remarkable morphological differences between *Ormosolenia* and *P. nebrodense*, such that the inclusion of the latter species into *Ormosolenia* is difficult to

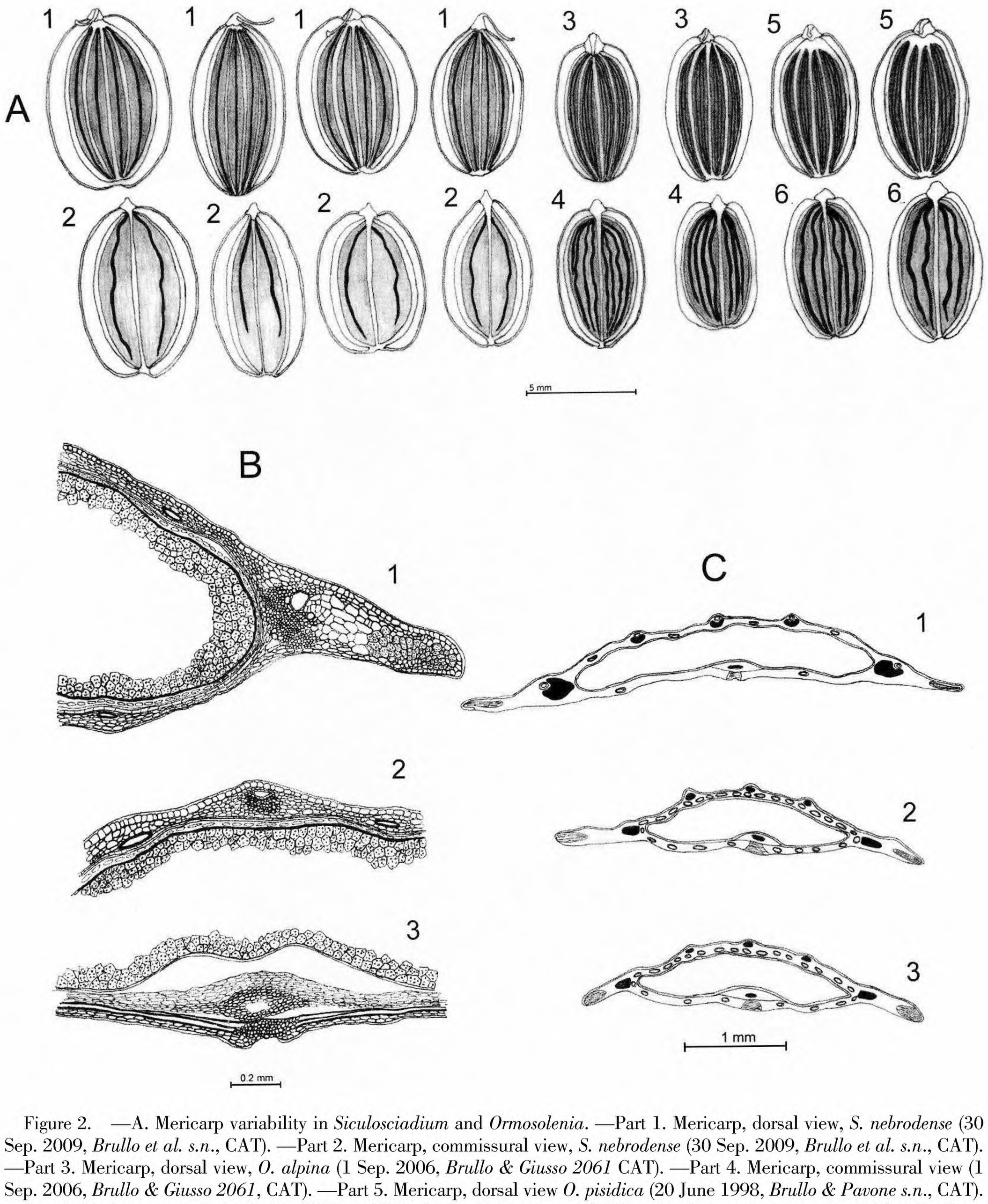
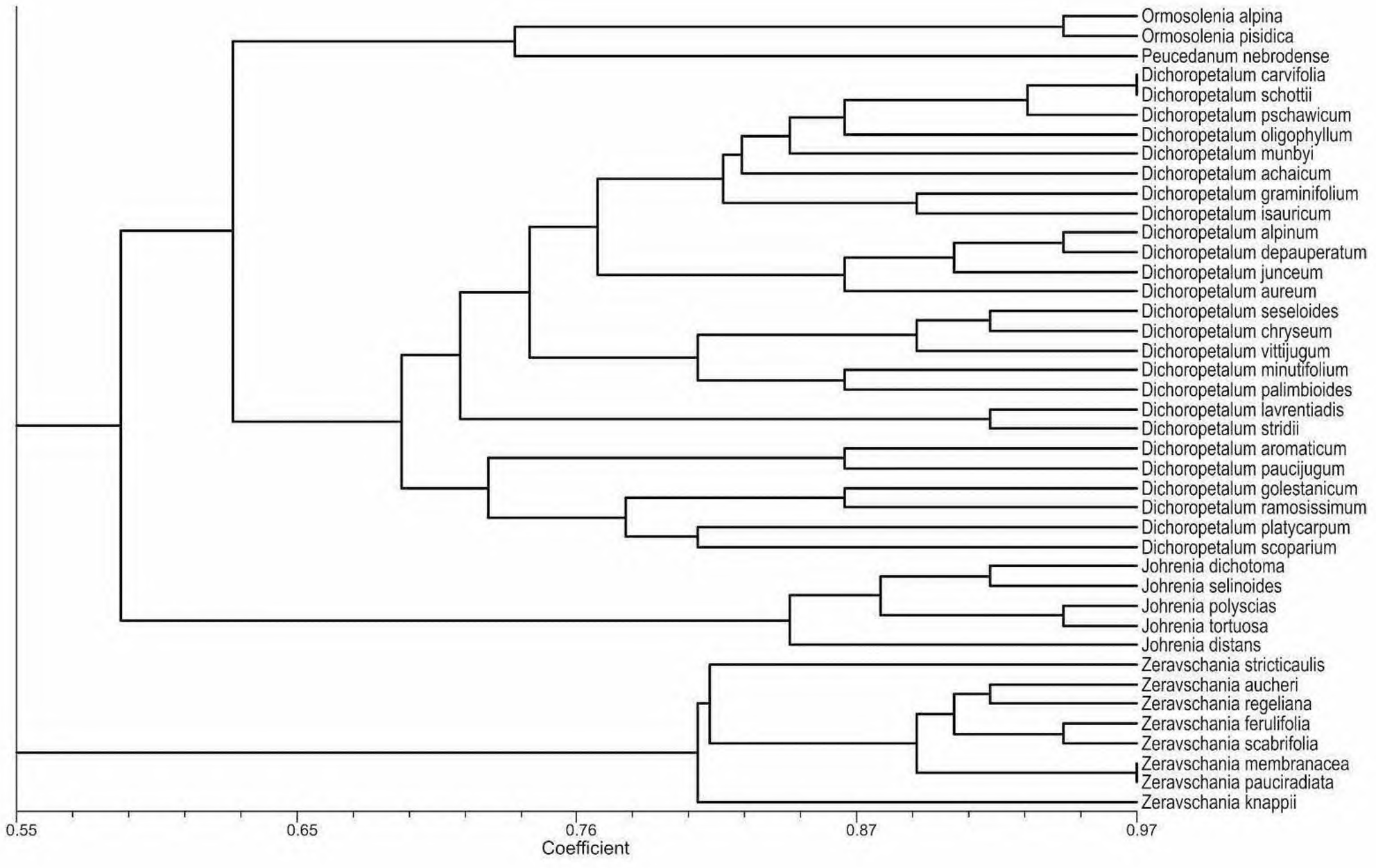
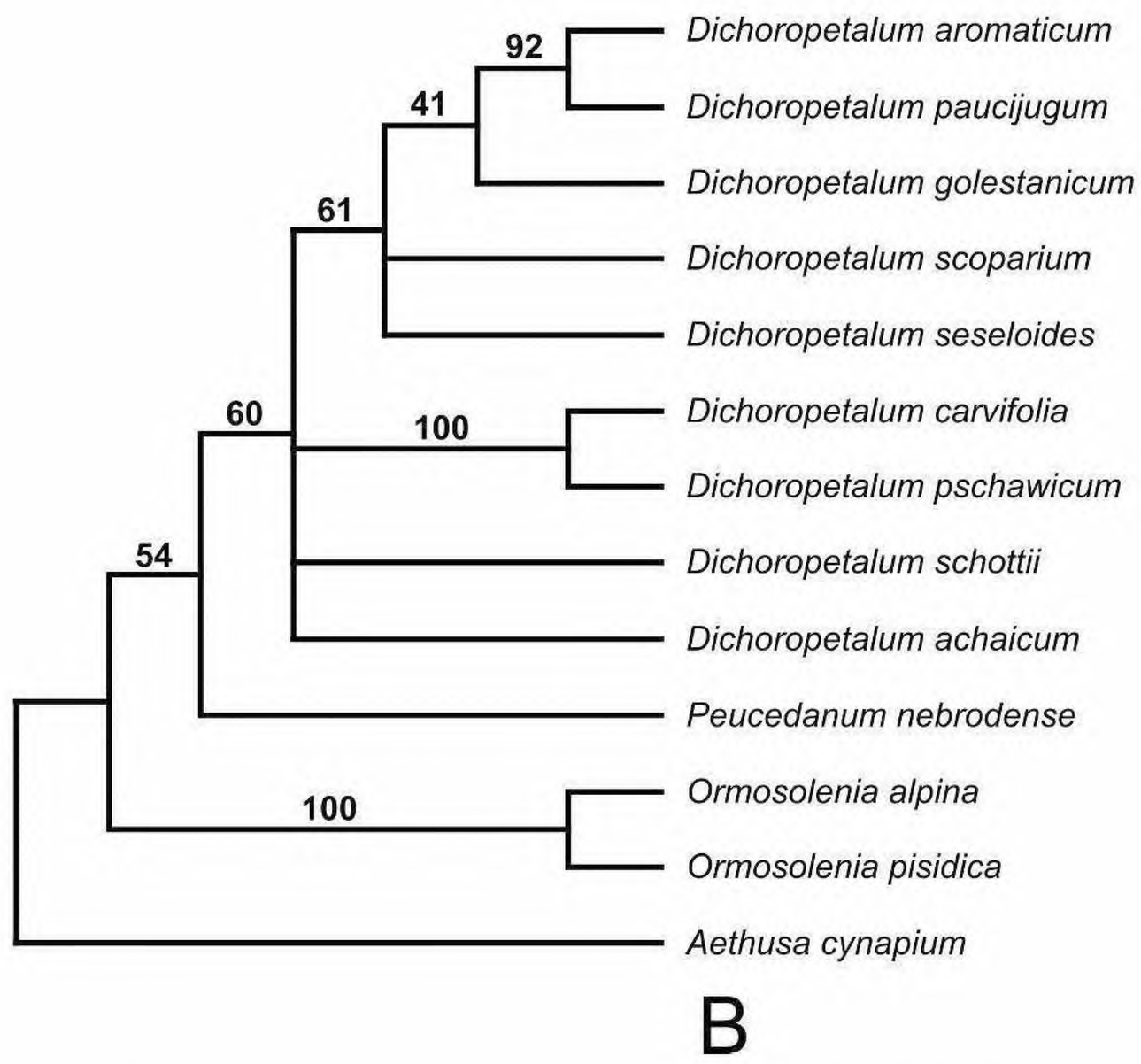


Figure 2. —A. Mericarp variability in *Siculosciadium* and *Ormosolenia*. —Part 1. Mericarp, dorsal view, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 2. Mericarp, commissural view, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 3. Mericarp, dorsal view, *O. alpina* (1 Sep. 2006, *Brullo & Giusso 2061* CAT). —Part 4. Mericarp, commissural view (1 Sep. 2006, *Brullo & Giusso 2061*, CAT). —Part 5. Mericarp, dorsal view *O. pisidica* (20 June 1998, *Brullo & Pavone s.n.*, CAT). —Part 6. Mericarp, commissural view (20 June 1998, *Brullo & Pavone s.n.*, CAT). —B. Mericarp cross sections of *S. nebrodense* (all living material from Madonie, Sicily). —Part 1. Mericarp, lateral view. —Part 2. Mericarp, dorsal central view. —Part 3. Mericarp, commissural central view. —C. Mericarp cross sections of *Siculosciadium* and *Ormosolenia*. —Part 1. Mericarp, *S. nebrodense* (30 Sep. 2009, *Brullo et al. s.n.*, CAT). —Part 2. Mericarp, *O. alpina* (1 Sep. 2006, *Brullo & Giusso 2061*, CAT). —Part 3. Mericarp, *O. pisidica* (20 June 1998, *Brullo & Pavone s.n.*, CAT).

accept upon the basis of these characters, several of which were not included in the phenetic analysis. These differences chiefly concern their ontogenetic cycle, life form, leaf shape, and petiole and fruit anatomy (Table 2). The genus *Ormosolenia* is characterized by a nonsuffruticose rootstock and basal leaves that are deciduous, reniform to ovate in outline, entire to 1-pinnate, and with up to one pair of leaflets. Its cauline leaves are usually absent. The petiole has five secretory ducts between the collenchyma and vascular bundles, the petals are yellowish green, the mericarps have three to six



A



B

Figure 3. —A. UPGMA phenogram showing the morphological relationships among the genera *Ormosolenia*, *Dichoropetalum*, *Johrenia*, *Zeravschania*, and *Siculosciadium*. —B. Strict consensus tree of ten 129-step trees resulting from maximum parsimony analysis of 17 parsimony informative morphological characters and DNA sequence data from the nrDNA ITS region. The numbers above the branches are bootstrap values.

Table 2. Comparative scheme of the distinguishing morphological characters of *Siculosciadium*, *Ormosolenia*, *Peucedanum*, *Dichoropetalum*, *Johrenia*, and *Zeravschania*.

Character	*Siculosciadium*	*Ormosolenia*	*Peucedanum* s. str.	*Dichoropetalum*	*Johrenia*	*Zeravschania*
Life form	polycarpic	polycarpic	polycarpic or monocarpic	polycarpic or monocarpic	monocarpic	polycarpic
Taproot	no	no	yes	yes	yes	yes
Leaf persistence	evergreen	deciduous	deciduous	deciduous	deciduous	deciduous
Rootstock	suffruticose	not suffruticose	not suffruticose	not suffruticose	not suffruticose	not suffruticose
Caudices	well developed	well developed	absent	absent	absent	absent
Fibrous collar	absent	absent	present	present	present	present
Basal leaves, insertion	apex of caudices	apex of caudices	apex of taproot	apex of taproot	apex of taproot	apex of taproot
Basal leaf blade, in outline	oblong to oblong-ovate	reniform to ovate	ovate to semicircular	triangular to lanceolate	triangular to ovate	triangular to ovate
Basal leaf shape	2-pinnate	entire to 1-pinnate	ternate to multisect	1- to 3-pinnate	2-pinnate	1- to 3-pinnate
Pairs of leaflets, number	3 to 4	absent to 1	3 to 5	1 to 6	1 to 6	1 to 3
Leaflet shape	ovate to deltoid	reniform to ovate	linear	linear to ovate	linear to lanceolate	ovate to ovate-oblong
Cauline leaves	present	usually absent	present	present	present or strongly reduced	present
Umbel rays, number	4 to 8	3 to 6	10 to 45	3 to 20	3 to 20	3 to 12
Bracts	absent	absent	absent to 3	absent	absent	(1)3 to 8
Bracteoles, number	1 to 5	absent to 2	2 to 10	1 to 5	1 to 5	2 to 8
Bracteoles, texture	herbaceous	setaceous	herbaceous	herbaceous	herbaceous	herbaceous
Bracteoles, relative to umbellulae	subequal to shorter	shorter	shorter	usually shorter	shorter	subequal to shorter
Calyx teeth	absent	inconspicuous	developed	inconspicuous	inconspicuous	inconspicuous to triangular
Petal color	white	yellowish green	yellow	white, yellow, pink	yellow	white (rarely yellowish white?)
Stylopodium	conical-flattened	conical-flattened	conical	flat to conical	flat to shortly conical	shortly conical
Mericarp wings	developed	short	developed	short to well developed	absent	short
Dorsal ribs	keeled	indistinguishable	filiform	filiform to inflated	indistinguishable	filiform
Vittae, per vallecula	1	3 to 6	1 to 3	absent to 3	absent to 3	1
Commissural vittae	2	4 to 8	2	absent to 4	absent to 4	2
Secretory ducts associated with vascular bundles	5	usually absent	absent	absent to 5	absent to 5	absent

vittae per vallecula and four to eight commissural vittae, the secretory ducts associated with vascular bundles are not always present, and the stylodium is shorter than the stylopodium. *Peucedanum nebrodense*, in contrast, has a suffruticose rootstock, basal leaves that are evergreen, oblong to oblong-ovate in outline, and 2-pinnate with three to four pairs of leaflets. Its cauline leaves are present. The petiole has four secretory ducts interposed among the vascular bundles, the petals are white, the mericarps have only a single vitta per vallecula and two commissural vittae, five secretory ducts are associated with its vascular bundles, and the stylodium is much longer than the stylopodium. Remarkable morphological differences are also apparent between *P. nebrodense* and other genera included in our comparative study, namely *Dichoropetalum* (including *Holandrea*), *Johrenia*, and *Zeravschania*. These differences are presented in Table 2, but are also reflected in the groupings of the UPGMA tree (Fig. 3A).

Ormosolenia pisidica is considered by Boissier (1849) as distinct from *O. alpina* by its better developed stems, nonthickened umbel rays, and yellow flowers. Subsequently, Boissier (1872) transferred both species to the genus *Peucedanum*, while more recently Chamberlain (1972), Hartvig (1986), and Pimenov (1992) treated *O. pisidica* as a synonym of *O. alpina*. In this study, both morphological and anatomical characters support the separation of *O. pisidica* from *O. alpina*. In particular, *O. pisidica* is characterized by stems 10–20(–30) cm tall, leaves 2–4 cm, umbels 3- to 4-rayed, umbellules 3- to 6-flowered, petals yellow, fructiferous pedicels thin and subequal to the fruit, and mericarps with filiform ribs and four(six) commissural vittae. *Ormosolenia alpina*, on the other hand, has stems 3–10(–15) cm tall, leaves 2–10 cm, umbels 4- to 7-rayed, umbellules up to 10-flowered, petals greenish white (often violet in bud), fructiferous pedicels thickened and shorter than the fruit, as well as mericarps with slightly inflated ribs and six to eight commissural vittae.

PHYLOGENETIC ANALYSES OF MOLECULAR AND MORPHOLOGICAL DATA

The data matrix of combined ITS sequence and morphological data for 13 species comprised 544 invariant, 43 autapomorphic, and 41 informative positions, the latter including 17 parsimony-informative morphological characters. Maximum parsimony analysis of these combined data resulted in ten 129-step trees (consistency indices = 0.7442 and 0.6071, including and excluding uninformative characters; retention index = 0.6452). Differences among these trees were restricted to the relative placements of several *Dichoropetalum* species. The strict consensus of these 10 trees is presented in Figure 3B. The results of this analysis support the recognition of *Dichoropetalum* as a monophyletic group (albeit the clade is weakly supported, with a 60% bootstrap value). The two species of *Ormosolenia* unite as a strongly supported clade (100% bootstrap value). *Peucedanum nebrodense* is sister to the *Dichoropetalum* clade, although this relationship is also weakly supported (54% bootstrap value), with only four or five molecular characters supporting this relationship, depending upon the tree. Constraining both species of *Ormosolenia* and *P. nebrodense* to monophyly and repeating the maximum parsimony analysis resulted in trees just one step longer than those without the constraint invoked. These results are inconclusive in establishing whether *P. nebrodense* is more closely related to *Dichoropetalum* or to *Ormosolenia*; indeed, *P. nebrodense* may actually comprise an isolated lineage separate from these two taxa upon the collapse of a single node. Further molecular data will be required to elucidate unequivocally the phylogenetic position of *P. nebrodense*.

CONCLUSIONS

The results of this study, incorporating data from morphology, karyology, fruit and petiole anatomy, and ontogeny, as well as results of both phenetic analysis of morphological data and phylogenetic analysis of combined morphological and molecular data, strongly support the recognition of *Peucedanum nebrodense* as a distinct taxon, closely allied to *Dichoropetalum* and *Ormosolenia*. An affinity to *Peucedanum* s. str. is not supported, nor is a close relationship to segregate taxa such as *Imperatoria* and *Pteroselinum*. Instead, maximum parsimony analysis of combined data suggests an affinity with *Dichoropetalum*, whereas the UPGMA tree, based largely upon characters selected by Pimenov et al. (2007) to discern among species of *Dichoropetalum*, *Johrenia*, and *Zeravschania*, suggests that *P. nebrodense* is more similar morphologically to *Ormosolenia*. Of these two analyses, we favor the maximum parsimony trees as indicating true relationship, but we acknowledge that branch support is weak and that further molecular studies incorporating chloroplast DNA will be necessary to confirm phylogenetic relationships among these taxa. Nevertheless, *Peucedanum nebrodense* can clearly be distinguished from *Ormosolenia* and *Dichoropetalum* upon a variety of characters, with many of these characters supporting its isolated position within the group. Furthermore, *P. nebrodense*

presents an isolated geographic distribution, known only from one population exclusively localized in a high mountain doline of the Madonie Massif. No other species examined herein occur in Sicily or in southern Italy. Therefore, we recognize *P. nebrodense* as comprising the new genus *Siculosciadium*. In order to highlight the morphological differences between this new genus and its putatively allied genera, the following analytical key is provided.

KEY TO THE CLOSELY RELATED GENERA OF *SICULOSCIADIUM*

1a. Rootstock not well developed with numerous long caudices, without fibrous collar; basal leaves inserted at apex of caudices.
  2a. Basal leaves 2-pinnate, with 3 to 4 pairs of ovate to deltoid leaflets; cauline leaves present; mericarps with 1 vitta per vallecula and 2 commissural vittae, with secretory ducts associated with vascular bundles ..... *Siculosciadium*
  2b. Basal leaves entire or 1-pinnate, with up to 1 pair of reniform to ovate leaflets; cauline leaves usually absent; mericarps with 3 to 6 vittae per vallecula and 4 to 8 commissural vittae, without secretory ducts associated with vascular bundles ..... *Ormosolenia*
1b. Rootstock robust without caudices, covered at the top by a fibrous collar; basal leaves inserted directly at apex of the rootstock.
  3a. Calyx teeth developed; leaf petiole round in cross section; leaf blade ternate-multisect, tridimensional, with primary segments long petiolate and ultimate segments entire, 2–9 cm ..... *Peucedanum* s. str.
  3b. Calyx teeth inconspicuous or very short; leaf petiole falcate in cross section with a ventral groove; leaf blade once to 3-pinnate, plane, with primary segments sessile or short petiolate and ultimate segments dentate or lobate (rarely entire), 0.5–2 cm.
    4a. Bracts (1 to)3 to 8; mericarps dorsally convex without occurrence of secretory ducts associated with vascular bundles ..... *Zeravschania*
    4b. Bracts absent; mericarps dorsally compressed usually with secretory ducts associated with vascular bundles.
      5a. Leaf sheath very long; mericarps with dorsal ribs indistinguishable and wings absent ..... *Johrenia*
      5b. Leaf sheath rather short; mericarps with dorsal ribs filiform to inflated (keeled) and wings more or less developed ..... *Dichoropetalum*

TAXONOMIC TREATMENT

I. Siculosciadium C. Brullo, Brullo, S. R. Downie & Giusso, gen. nov. TYPE: *Siculosciadium nebrodense* (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso

Genus novum *Ormosoleniae* Tausch affine, a qua caudice suffruticoso sempervirenti, foliis basalibus bipinnatis segmentis lateralibus ambitu oblongis vel oblongo-ovatis segmento terminali laterales subaequenti vel quam eis minore, foliis caulinis praesentibus, bracteolis umbellularum 1 ad 5 herbaceis margine hyalinis, dentibus calycinis nullis, petalis albis colore roseo-purpurascenti suffusis apice truncatis, strato interno mesocarpii ex cellularum prosenchymatarum serie una et cellularum collenchymatarum serie una constanti, quaque vallecula vitta valleculari solitaria et vittis commissuralibus duabus praedita, canaliculis jugalibus solitariis atque stylodio in fructu bene evoluto reflexo quam stylopodio per anthesin multo longiore differt.

Evergreen polycarpic dwarf shrub; rootstock branched, covered by a thin rhytidome, without fibrous collar; stems numerous, leafy, erect to ascending, usually with umbels at the nodes. Basal leaves petiolate, inserted in the terminal part of the caudices; sheath linear, whitish; blade 2-pinnate, with 3 to 4 pairs of leaflets, terminal leaflet subequal or smaller than the lateral ones; lobes oblong to ovate, rounded at apex; cauline leaves becoming increasingly smaller upward, petiolate to sessile; blade 1- or 2-pinnate; lobes linear to linear-lanceolate. Inflorescence composed of long pedunculate compound umbels, unequally rayed; bracts absent; umbellule with 1 to 5 bracteoles, herbaceous with hyaline margin, subequal to or shorter than rays. Flowers hermaphrodite or masculine, pedicellate; calyx teeth absent; petals white, tinged with pink purplish outside, inflexed, thick, truncate at apex; stylopodium conical-flattened. Mericarps lenticular, shallowly compressed dorsally with well-distinct spongy wings, 5-ribbed, 3 of which are dorsal and 2 marginal; exocarp 1-layered; mesocarp 2-layered, its outer layer consisting of parenchymatous cells; inner layer of mesocarp consisting of 1 row of prosenchymatous cells and 1 row of collenchymatous cells; vascular bundles 5; five secretory ducts associated with vascular bundles, 4 more are vallecular and 2 commissural not reaching the base. Stylodium in fruit well developed, reflexed, and much longer than the stylopodium in flower.

1. Siculosciadium nebrodense (Guss.) C. Brullo, Brullo, S. R. Downie & Giusso, comb. nov. Basionym: *Pteroselinum nebrodense* Guss., Fl. Sicul. Syn. 1: 336. 1844. *Imperatoria chabraei* Guss., Fl. Sic. Prodr. 1: 368. 1827, nom. illeg., non *Imperatoria chabraei* Spreng., Sp. Umbell.: 64. 1818. *Peucedanum nebrodense* (Guss.) Nyman, Syll. Fl. Eur.: 153. 1855. *Peucedanum nebrodense* (Guss.) Strobl, Flora 69(36): 567. 1886. *Peucedanum carvifolia* (L.) Vill. var. *nebrodense* (Guss.) Paol. in Fiori & Paol., Fl. Anal. Ital. 2: 179. 1900.

Holandrea nebrodensis (Guss.) Banfi, Galasso & Soldano, Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano 146(2): 233. 2005. TYPE: [Italy, Sicily. Palermo:] Sub *Pteroselinum nebrodense*, Madonie, alle Fosse di S. Gandolfo, julio [manu Gussone], (lectotype, designated here, NAP-GUSS!; isolectotype, FI!). Figure 4.

Dwarf glabrous perennial, polycarpic, suffruticose, rhizomatous, evergreen, with a well-developed creeping and branched rootstock, 4–12 cm, 2–5 mm diam., covered by a thin, pale brown rhytidome; fibrous collar absent; stems numerous, leafy, erect to ascending, 15–30 cm tall, usually with umbels at the nodes. Basal leaves green, glaucous, 5–15 cm, inserted in the terminal part of the caudices; sheath long linear, whitish, 1–2.5 cm × 3–5 mm; petiole slightly striate, 1.5–7 cm; blade oblong to oblong-ovate in outline, flat, 1.5–6 × 1–3 cm, 2-pinnate, with 3 to 4 pairs of leaflets, ovate to deltoid, ± incised, terminal leaflet subequal or smaller than the lateral ones; lobes oblong to ovate, rounded at apex with hyaline mucro; primary lobes 6–17 mm and secondary lobes 3–11 mm; cauline leaves becoming increasingly smaller upward with petiole 0–25 mm; sheath 2–5.5 cm × 2–4 mm; blade lanceolate to triangular in outline, 1- or 2-pinnate; lobes linear to linear-lanceolate, primary ones 5–22 mm and secondary ones 5–13 mm, usually acute at apex. Inflorescence composed of long pedunculate compound umbels, unequally 4- to 8-rayed, rays 0.5–1.5 cm; bracts absent; flexuous when flowering, rigid when fruiting; umbellule with 1 to 5 bracteoles, subulate, herbaceous with hyaline margin, subequal to or shorter than rays. Flowers hermaphrodite or masculine, 4 to 8 per umbellule, 2–2.2 mm diam., pedicellate; calyx teeth absent; petals ovate, 1.5 mm, white tinged with pink purplish outside, inflexed, thick, truncate at apex; stamens long exserted, inrolled, wholly white; staminal filament 1.7 mm; anther 0.5 mm; stylopodium conical-flattened; stylodium ca. 1 mm long, cylindrical, erect; ovary subcylindrical to obovoid, 1–1.2 mm. Mericarps subrounded to elliptical, lenticular, 6–8.5 × 4–5 mm, shallowly compressed dorsally with well-distinct spongy wings, 0.5–0.8 mm wide, 5-ribbed, 3 of which are dorsal and 2 marginal; exocarp 1-layered, interrupted near the ventral part of the wings; mesocarp 2-layered, its outer layer consisting of parenchymatous cells with thin walls; in the distal part of the wings these cells have slightly lignified walls with chinked pores; the inner layer of mesocarp consisting of 1 row of tangentially elongated prosenchymatous cells with slightly lignified walls; endocarp consisting of 1 row of collenchymatous cells; vascular bundles 5 (3 small and dorsal and 2 big and at the wing base); 5 secretory ducts associated with the vascular bundles, 4 more are vallecular and 2 commissural not reaching the base; endocarp 1-layered; endosperm ventrally flat. Stylodium in fruit elongating to ca. 2 mm, slender, reflexed, curved, and much longer than the stylopodium.

Distribution and ecology. This Italian species is exclusively found in the Madonie Massif on the island of Sicily, where it grows on the southern slopes of a dolina near Pizzo Carbonara, locally known as Fosse di S. Gandolfo. It grows at an altitude of about 1870 m.s.m. on Mesozoic carbonatic substrates, within a dwarf shrubby plant community characterized by several endemic chamaephytes and hemicryptophytes (Brullo et al., 2005), e.g., *Astragalus nebrodensis* (Guss.) Strobl (Fabaceae), *Erysimum bonannianum* C. Presl (Brassicaceae), *Acinos alpinus* (L.) Moench subsp. *nebrodensis* (Kerner & Strobl) C. Brullo & Brullo (Lamiaceae), *Minuartia verna* (L.) Hiem subsp. *grandiflora* (C. Presl) Hayek (Caryophyllaceae), *Petrorhagia saxifraga* (L.) Link subsp. *gasparrini* (Guss.) Greuter & Burdet (Caryophyllaceae), *Centaurea parlatoris* Heldr. (Asteraceae), *Cerastium tomentosum* L. (Caryophyllaceae), *Herniaria microcarpa* C. Presl (Illecebraceae), and *Silene sicula* Ucria (Caryophyllaceae).

Phenology. *Siculosciadium nebrodense* has been observed in flower from July to August, and in fruit from August to October.

Etymology. *Siculosciadium* comes from the Greek words "siculo," referring to "Sicilian," and "sciadion," referring to "umbel."

IUCN Red List category. *Siculosciadium nebrodense* is represented by few individuals, usually forming a thick layer and occupying a surface area of about 1000 m^2. For this reason, we propose to include this species in the Red List of Threatened Species as Critically Endangered (CR). Based on the criteria adopted by IUCN (2001, 2003, 2005), we herein proposed its inclusion in the following categories: CR B2ab(ii, iii, iv, v), C1.

Additional specimens examined. ITALY, SICILY. **Palermo:** Madonie, Fosse di S. Gandolfo, s.d., manu Gussone, sub *Pteroselinum nebrodense* (NAP-GUSS); in pascuis montosis Madonie, July, *Citarda 1450* (FI, PAL), 1 Sep. 1881, *Lojacono 223* (FI); Madonie, Fosse di S. Gandolfo e Vallone Reale, *Tineo* (FI); Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 9 Sep. 2001, *S. Brullo, G. Giusso del Galdo & S. Sciandrello s.n.* (CAT); Madonie, Pizzo Carbonara, Fosse di S. Gandolfo, 24 July 2002, *S. Brullo, G. Giusso del*

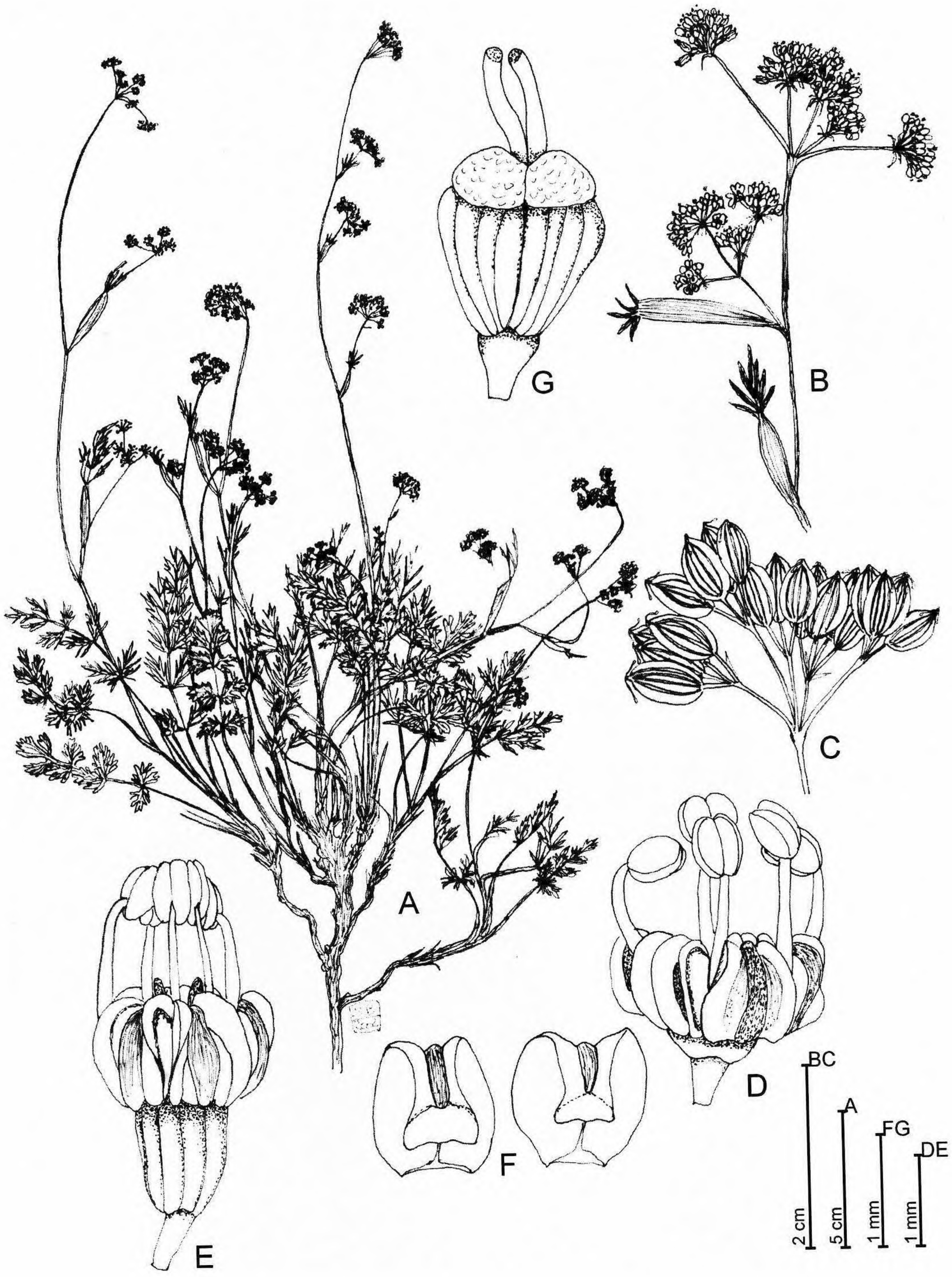


Figure 4. *Siculosciadium nebrodense*. —A. Flowering plant habit. —B. Inflorescence. —C. Fructified umbel. —D. Male flower. —E. Hermaphrodite flower. —F. Two petals, internal view. —G. Pistil. Living material taken from Madonie, Sicily, and drawn from the collection, 9 Sep. 2001, *S. Brullo, G. Giusso & S. Sciandrello s.n.* (CAT).

Galdo & S. Sciandrello s.n. (CAT), 30 Sep. 2009, *C. Brullo, S. Brullo & G. Giusso del Galdo s.n.* (CAT).

Specimens examined for Ormosolenia alpina. GREECE. **Crete:** in summis montibus Sphacioticas [Stravopodia] Creta, 10 July 1846, *Heldreich*, sub *Peucedamum creticum* (WU); in summis alpinis Sphakiottleis, s.d., *Sieber*, sub *P. creticum* (G-DC); in Crete, s.d., *Sieberus*, sub *Sison alpina* (B); n. M. altis Sphakiott, s.d., *Sieber*, sub *S. alpinum* (G); Creta, inter lapidis summi inter Stravopodia, 10 July 1846, *Heldreich*, sub *Ormosolenia cretica* (G-BOISS, G); Crete, hautes montagnes de Sphakia, June 1845, *Raulin 485* (G-BOISS); Creta, Distr. Sphakia, Levka Ori, in glareosis calc. montis Pachnes, 16 June 1942, *Rechinger 13848* (G); Crete, Ep. Sphakia, 20 Sep. 1966, *Greuter 7551* (G); Crete, Sfakia, 20 km above Anopoli to top of Mt. Pachnes, 12 July 1993, *Bergmeier & Matthas 3416* (B); Griechenland, Nomos Hanion, Eparchia Sfakion, Lefka Ori, Pahnes-Gipfel, 7 Aug. 1998, *Böhling 8750* (B); Crete, Lefka Ori, Trocharis, 26 Aug. 2003, *Bacchetta & Brullo* (CAT); Crete, Lefka Ori, Mt. Pachnes, 1 Sep. 2006, *Brullo & Giusso del Galdo 2061* (CAT).

Specimens examined for Ormosolenia pisidica. TURKEY. Dans la region alpine de Mt. Stravros près d'Isparte, 10 Aug. 1845, *Boissier* (G-BOISS); Davraz Dag, 20 June 1998, *Brullo & Pavone s.n.* (CAT). **C2:** Mugla, Koycegeiz, Sandras Da. Besparmak Tepesi, 5 Sep. 1978, *N. & E. Ozhatay 41501* (G). **C3:** Pisidien, Isparta, 2 July 1948, *Renz 8704* (G); Anatolia, Distr. Kemer, Tahtali Dag, 16 Aug. 1947, *Davis 14196* (G); Anatolia, Tahtali Dag (ca. 50 km SW Antalya), W side, (ascent from village of Yukari Beycik) rocky slope & scree, 17 July 1984, *Gork, Hartvig & Strid 23599* (B, G).

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APPENDIX 1. List of 36 morphological characters and character states included in the morphological matrix used in the phenetic analysis.

1. Habit: 0, monocarpic with unbranched rootstock; 1, polycarpic with branching rootstock.
2. Leaf petioles at stem base: 0, present (at least as dense remnants); 1, absent.
3. Stem height: 0, 7–40 cm; 0.5, 41–100 cm; 1, exceeding 100 cm.
4. Stem ribs: 0, without prominent ribs; 1, with ± prominent ribs.
5. Stem pubescence: 0, glabrous; 1, pubescent.
6. Leaf shape: 0, linear to lanceolate; 0.5, subrounded to reniform; 0.75, oblong to oblong-ovate; 1, ovate to triangular.
7. Leaf sheath relative length: 0, long; 1, short.
8. Leaf sheath shape: 0, linear; 1, triangular.
9. Leaf basal primary segments: 0, sessile; 0.5, with petiole less than 5 mm; 1, with petiole exceeding 5 mm.
10. Shape of terminal leaf lobes: 0, filiform or linear; 0.5, lanceolate; 1, ovate.
11. Terminal leaf lobes: 0, clustered; 1, not clustered.
12. Upper cauline leaves: 0, absent; 1, present.
13. Bracts: 0, present; 1, absent.
14. Mininum number of rays per umbel: 0, fewer than 5; 1, equal to or more than 5.
15. Maximum number of rays per umbel: 0, < 10; 1, > 10.
16. Umbel rays, relative proportions: 0, very unequal; 0.5, slightly unequal; 1, almost equal.
17. Bractlet texture: 0, completely herbaceous, 1, with narrow white margins.
18. Bractlet shape: 0, subulate to linear; 0.5, linear-lanceolate; 1, lanceolate to broadly lanceolate.
19. Bractlets/umbellules, relative proportions: 0, bractlets longer than umbellules, 1, shorter than umbellules.
20. Calyx teeth: 0, present; 1, absent.
21. Petals color: 0, white; 1, yellow.
22. Stylopodium shape: 0, flat; 0.5, short-conical; 1, conical.
23. Mericarps shape: 0, dorsally convex; 1, dorsally compressed.
24. Dorsal mericarp ribs: 0, indistinguishable; 0.5, filiform; 0.75, keeled or slightly inflated; 1, strongly spongy inflated.
25. Marginal mericarp ribs: 0, not developed; 1, ± developed.
26. Mericarp parenchyma (commissural side): 0, with destroyed parenchyma near carpophore; 1, commissural parenchyma not destroyed.
27. Parenchyma cells with lignified pitted walls on dorsal mericarp side: 0, developed; 1, absent or sometimes only under vascular bundles.
28. Marginal ribs inflated: 0, composed of large mesocarp cells with lignified pitted walls; 1, without lignified pitted walls.
29. Inner lignified layer of mesocarp (hypendocarp): 0, absent; 0.5, faintly marked; 1, strongly expressed.
30. Secretory ducts (vittae) in mericarp furrows, presence: 0, absent or inconsistent, not visible in each furrow; 1, always developed.
31. Secretory ducts (vittae) in mericarp furrows, organization: 0, solitary; 1, several in each furrow.
32. Commissural secretory ducts (vittae): 0, absent; 0.5, two in each mericarp; 1, more than two per mericarp.
33. Rib secretory ducts: 0, absent; 1, present.
34. Mericarp vascular bundle organization and number: 0, compact; 1, consisting of several groups of vascular elements.
35. Leaf persistence: 0, deciduous; 1, evergreen.
36. Rootstock habit: 0, not suffruticose; 1, suffruticose.

Appendix 2. Data matrix of the 36 morphological characters used for the phenetic analysis. Character and coding character states correspond to those in Appendix 1.

Taxa	Character states for characters 1–36																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Dichoropetalum achaicum (Halácsy) Pimenov & Kljuykov	1	0	0	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	1	1	1	1	1	0.5	1	1	1	0	1	1	0	1	1	0	0	0
Dichoropetalum alpinum Fenzl	1	0	0	0	0	1	1	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum aromaticum (Rech. f.) Pimenov & Kljuykov	0	0	0.5	1	0	0	1	1	0	1	1	1	1	1	0	0	0	0	1	1	1	0.5	1	1	1	1	0	0	0.5	0	0	0	1	0	0	0
Dichoropetalum aureum (Boiss. & Balansa) Pimenov & Kljuykov	1	0	0	0	0	1	1	0	0	0.5	0	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0	1	0	0	0
Dichoropetalum carvifolia (Vill.) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum chryseum (Boiss. & Heldr.) Pimenov & Kljuykov	0	0	0.5	1	0	0	1	0	0	0.5	1	1	1	1	1	0	0	0	1	1	1	0.5	1	0.5	1	1	1	0	0.5	1	0	0.5	1	0	0	0
Dichoropetalum depauperatum (Boiss. & Balansa) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0.5	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum golestanicum (Rech. f.) Pimenov & Kljuykov	0	0	0.5	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	1	1	0.5	1	1	0	0	1	1	0	0	1	0	0	0
Dichoropetalum graminifolium (Boiss.) Pimenov & Kljuykov	0	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	0	0	0	1	1	0	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum isauricum (Parolly & Nordt) Pimenov & Kljuykov	0	0	0.5	0	0	1	1	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0.5	1	0.75	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum junceum (Boiss.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	0.5	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.5	1	1	1	0	1	1	0	0.5	0	0	0	0
Dichoropetalum lavrentiadis (Strid & Papan.) Pimenov & Kljuykov	1	0	0	1	0	1	1	0	0	0.5	1	1	1	1	0	0.5	0	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	1	0	0.5	1	0	0	0
Dichoropetalum minutifolium (Janka) Pimenov & Kljuykov	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum munbyi (Boiss.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	0	0.5	1	0	1	0	0	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	0	0	1	0	0	0
Dichoropetalum oligophyllum (Griseb.) Pimenov & Kljuykov	0	0	0	0	0	1	1	0	0	0.5	1	0	1	1	0	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	0.5	1	0	0	0
Dichoropetalum palimbioides (Boiss.) Pimenov & Kljuykov	0	0	0.5	0	1	0	1	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	0.5	1	0.75	1	1	1	0	0.5	1	1	1	1	0	0	0
Dichoropetalum paucijugum (DC.) Pimenov & Kljuykov	0	0	0	1	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	0	0	0.5	0	0	0	1	0	0	0
Dichoropetalum platycarpum (Boiss.) Pimenov & Kljuykov	1	0	0.5	0	1	0	1	0	0	0.5	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0
Dichoropetalum pschawicum (Boiss.) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	1	1	1	1	0	0	0	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum ramosissimum (Mozaff.) Pimenov & Kljuykov	0	0	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	1	1	0.5	1	0.5	1	1	0	0	1	0	0	0	0	0	0	0

Appendix 2. Continued.

Taxa	Character states for characters 1–36																																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Dichoropetalum schottii (Bess) Pimenov & Kljuykov	1	0	0.5	0	0	1	1	0	0	0.5	1	0	0	1	1	0	0	0	1	1	0	0.5	1	0.5	1	1	1	0	1	1	1	1	1	0	0	0
Dichoropetalum scoparium (Boiss.) Pimenov & Kljuykov	1	0	1	0	1	0	1	0	0	0.5	1	0	1	0	0	0	0	0	1	1	1	1	1	0.5	1	1	1	0	0.5	1	1	0	1	0	0	0
Dichoropetalum seseloides (C. A. Mey.) Pimenov & Kljuykov	0	0	0.5	0	0	0	1	0	0	0.5	1	1	1	1	1	0	0	0	1	1	1	1	1	0.5	1	1	1	0	1	1	0	0.5	1	0	0	0
Dichoropetalum stridii (Hartvig) Pimenov & Kljuykov	1	1	0	1	0	1	1	0	0	0.5	1	1	1	1	0	0.5	0	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	0	0	0	1	0	0	0
Dichoropetalum vittijugum (Boiss.) Pimenov & Kljuykov	0	0	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	0	1	1	1	0	1	0.5	1	1	1	0	1	1	0	0.5	1	0	0	0
Johrenia dichotoma DC.	0	1	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia distans (Griseb.) Halácsy	0	1	0.5	0	0	1	0	0	0	0.5	1	1	1	0	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Johrenia polyscias Bornm.	0	1	0.5	0	0	1	0	0	0.5	0.5	1	1	1	1	0	0	0	0	1	1	1	0.5	1	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia selinoides Boiss. & Balansa ex Boiss.	0	1	1	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Johrenia tortuosa (Fisch. & C. A. Mey.) Chamberlain	0	1	1	0	0	1	0	0	0.5	0.5	1	1	1	1	0	0	0	0	1	1	1	0.5	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Ormosolenia alpina (Sieber ex Schult.) Pimenov	1	1	0	1	0	0.5	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0.5	1	0	1	1	1	0	0.5	1	1	1	1	0	0	0
Ormosolenia pisidica Boiss. & Heldr.	1	1	0	1	0	0.5	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0.5	1	0.5	1	1	1	0	0.5	1	1	1	1	0	0	0
Peucedanum nebrodense (Guss.) Nyman	1	1	0	1	0	0.75	0	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0.5	1	0.75	1	1	1	0	0.5	1	0	0.5	1	0	1	1
Zeravschania aucheri (Boiss.) Pimenov	1	0	0.5	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania ferulifolia (Gilli) Pimenov	1	0	0.5	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania knappii (Bornm.) Pimenov & Kljuykov	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	1	0	0	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	1	0	0	0
Zeravschania membranacea (Boiss.) Pimenov	1	0	1	0	0	1	1	1	1	0	1	1	0	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania pauciradiata (Tamamsch.) Pimenov	1	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania regeliana Korovin	1	0	0.5	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0.5	0	0.5	1	1	1	1	1	1	0	0.5	1	0	0	0
Zeravschania scabrifolia Pimenov	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0
Zeravschania stricticaulis (Rech. f.) Pimenov & Kljuykov	1	0	0.5	0	1	1	1	0	0	0.5	1	1	0	0	0	1	1	1	1	0	1	0.5	0	0.5	1	1	1	1	1	1	0	0.5	0	0	0	0

Appendix 3. List of 17 morphological characters and associated character states used in the phylogenetic analysis

1. Habit: 0, monocarpic with unbranched rootstock; 1, polycarpic with branching rootstock.
2. Stem base: 0, densely covered by remains of leaf petioles; 1, without remains of petioles.
3. Stem height (in cm): 0, 7–40; 1, 41–100; 2, more than 100.
4. Stem ribs: 0, without prominent ribs; 1, with ± prominent ribs.
5. Leaf shape: 0, linear to lanceolate; 1, subrounded to reniform; 2, oblong to oblong-ovate; 3, ovate to triangular.
6. Leaf sheath length: 0, long; 1, short.
7. Leaf sheath shape: 0, linear; 1, triangular.
8. Shape of terminal leaf lobes: 0, filiform to linear; 1, lanceolate; 2, ovate.
9. Calyx teeth: 0, absent; 1, present.
10. Petal color: 0, more white; 1, more yellow.
11. Stylopodium shape: 0, flat; 1, short-conical; 2, conical.
12. Dorsal mericarp ribs: 0, indistinguishable; 1, filiform; 2, keeled or slightly inflated; 3, strongly spongy inflated.
13. Marginal mericarp ribs: 0, not developed; 1, ± developed.
14. Parenchyma cells with lignified pitted walls on dorsal mericarp side: 0, developed; 1, absent or sometimes only under vascular bundles.
15. Secretory ducts (vittae) in mericarp furrows: 0, absent or inconsistent, not visible in each furrow; 1, always developed.
16. Commissural secretory ducts (vittae): 0, absent; 1, two in each mericarp; 2, more than two per mericarp.
17. Rib secretory ducts: 0, absent; 1, present.

Appendix 4. Data matrix of the 17 morphological characters used for the phylogenetic analysis. Characters and the coding of character states correspond to those in Appendix 3.

Taxa	Character states for characters 1–17																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Aethusa cynapium	0	1	2	1	3	1	0	2	0	0	1	3	0	1	1	1	0
Dichoropetalum achaicum	1	0	0	0	3	1	0	2	0	1	2	1	1	1	1	2	0
D. aromaticum	0	0	1	1	0	1	1	1	0	1	1	3	0	0	0	0	1
D. golestanicum	0	0	1	0	0	1	1	1	0	1	2	1	1	0	1	0	0
D. paucijugum	0	0	0	1	0	1	0	1	0	1	0	3	0	0	0	0	1
D. pschawicum	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
D. schottii	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
D. scoparium	1	0	2	0	0	1	1	0	0	1	2	1	1	1	1	0	0
D. seseloides	0	0	1	0	0	1	0	0	0	1	2	1	1	1	1	1	1
D. carvifolia	1	0	1	0	3	1	0	0	0	0	1	1	1	1	1	2	0
Ormosolenia alpina	1	1	0	1	1	0	0	2	1	0	1	0	1	1	1	2	0
O. pisidica	1	1	0	1	1	0	0	2	1	1	1	1	1	1	1	2	0
Peucedanum nebrodense	1	1	0	1	2	0	0	2	0	0	1	2	1	1	1	1	0

FLOWER-VISITING RECORDS OF THE NATIVE BEES OF NEW CALEDONIA[1]

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ABSTRACT

The flower-visiting records for the 43 species of bees considered to be native to New Caledonia show that females of 21 species visited 116 native species of plants in 69 genera and 41 families, and the bees were documented to carry pollen from 64 species and possibly four more. The plant families with the greatest number of species documented for visits by female bees were, in descending order: Myrtaceae (21), Dilleniaceae (10), Cunoniaceae (nine), Araliaceae (seven), Fabaceae (seven, encompassing the Caesalpinioideae, Mimosoideae, and Papilionoideae), Goodeniaceae (five), Proteaceae (five), Apocynaceae (four), Sapindaceae (four), and remaining families with one to three species. Females of six and possibly one more species carried pollen from each of Dilleniaceae and Myrtaceae, six carried pollen from Araliaceae, five from Goodeniaceae, four and possibly one more from Cunoniaceae, four from each of Fabaceae and Sapindaceae, and none to three from the remaining 34 families observed. For introduced plants, female bees of 12 species visited 54 species in 43 genera among 19 plant families and were documented to carry pollen from 31 and possibly one more species. For introduced plants, families with the highest number of species visited by female bees, in descending order, were: Asteraceae (12); Fabaceae (eight); Verbenaceae (seven); and Euphorbiaceae, Myrtaceae, and Solanaceae each with three. The remaining 13 families had either one or two species visited by bees. Females of seven species of bees carried pollen from Fabaceae, six from Asteraceae, three each from Myrtaceae and Solanaceae, and none to "2 + 1?" (two or possibly three) from remaining families. Only half a dozen species of native bees can be considered to be common, in that they can be expected to be observed reasonably regularly on a range of flowers. The ubiquitous introduced honey bee *Apis mellifera* L. and its constant foraging for nectar and pollen on a very wide range of flowers may outcompete many species of native bees, potentially reducing their numbers, and consequently obscuring their relationships with the flora.

Key words: Apis, Araliaceae, competitive foraging pressure, Cunoniaceae, Dilleniaceae, Fabaceae, flower-visiting records, Goodeniaceae, introduced honey bee, Myrtaceae, native bees, New Caledonia, Proteaceae.

For a land mass of 19,103 km^2, New Caledonia is considered unique based on the high number of flowering plant species (3051) and its high endemicity (77.7%; Morat et al., 2012), which markedly contrasts with the low number of bee species (28 species, Donovan, 1983; 21 species, Pauly & Munzinger, 2003). A major question for evolutionary biologists is how so many distinctive species of flowering plants could have evolved with so few apparent pollinating bees. This includes a relative paucity of other pollinating insects, birds, and reptiles (Kato & Kawakita, 2004). In contrast, the number of known species of bees has about doubled in recent years. Taxonomic revisions of the major bee groups are currently underway, but will be time consuming, and yet there is much interest in the relationships between the various species of bees and flowering plants. The purpose of this study is to make available now all bee flower-visiting data. Observations for *Apis mellifera* L. are explicitly excluded because this honey bee was purposely introduced in 1848 (Lamaignere, 2001) and is not a naturally occurring constituent of the flower-visiting Apoidea. The term "native" for the remaining species of bees is used here to indicate those species that were likely present before the arrival of any humans about several thousand years ago (Irwin, 2010), and also those that might not have been knowingly introduced by humans. However, in the absence of intensive surveys of the bees of lands of the Southwest Pacific,

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Figure 1. Two female *Homalictus risbeci* (Cockerell, 1929) (the two small bees) and a female *Austronomia sicheli* (Vachal, 1897) (the large bee) visiting the flowers of *Dracophyllum verticillatum* Labill (Ericaceae), Col d'Arama, New Caledonia, 29 July 2005. Photograph by J. Munzinger.

the true status of many species may be uncertain (Groom & Schwarz, 2011).

Methods

Bees from New Caledonia from all known collections worldwide were borrowed, and flower data were recorded from labels attached to the pins. In addition, bees were collected with insect nets from flowers on Grande Terre during December 1979 and April to May 1981, and Grande Terre and Ile des Pins during October 1980 by B. J. Donovan and G. McPherson; on Grande Terre during January and May 1999, March to April 2001, November to December 2001, November to December 2002, and January 2004 by J. Munzinger; on Grande Terre during November to December 2000 by B. J. Donovan, H. Fortune, and J. Bradford; and Grande Terre and Lifou during July to August 2003 by B. J. Donovan. Since April 2004 to September 2008, bees have been collected at various times of year throughout New Caledonia by J. Munzinger (Fig. 1). The identity of flowers from which bees were collected was recorded on site, or if the flower could not be identified, specimens were taken for later study and identification; these vouchers were deposited in the herbaria of MO and NOU.

Bees were examined microscopically and where possible were identified to species, or if identification was not possible, numbered as separate taxa. The names of species of bees are as in Michener (2007), with the exception of the insect genus *Lipotriches* Gerstaecker, which is now referred to as *Austronomia* Michener. In Tables 1 and 3, the families, genera, and species of bees are ordered as in Michener (2007). As revisions of groups of bees are published (Donovan, in prep.; Pauly, in prep.), references in those works will be made to the species that are numbered in this study. For all species of bees, holotypes were examined wherever possible, and for species of bees named from areas beyond New Caledonia, voucher specimens were examined from New Caledonia. Data for voucher specimens are presented after the holotype data. Female bees were examined microscopically for evidence of pollen in scopae. When pollen is abundant the bee has obviously been collecting pollen for a while, but if a bee has just begun collecting pollen, very little may be evident. If scopae held very little pollen and it was no more abundant than on other parts of the bee, the bee was not considered to have been collecting pollen. However, if the pollen in scopae was at least partly clumped, the bee was considered to have been

collecting pollen. Female hylaeine and euryglossine bees carry pollen internally, so if they were captured in association with flowers, whether they were collecting pollen could not be readily ascertained. Females of an undescribed cleptoparasitic species, which is referred to in Tables 1 and 3 as "*Lasioglossum* sp. indet. 9," do not carry pollen. Notations such as "2/5 p" (Table 1) indicate that there were two collections of a total of five bees, all of which were carrying pollen, while "2/5 (1/3 p)" refers to two collections of a total of five bees, of which one collection of three bees was carrying pollen. The notation "0/1" indicates that one bee was observed on a flower. In this article, a notation such as "4 + 1?" means that females of four species of bees were carrying pollen, and possibly also the females of one species that carry pollen internally. A "collection" refers to an event during which bees were captured, and differs from another "collection" in at least one datum, such as the collector, the host plant, the site, or time of day. Because bees can fly rapidly, will sometimes visit a range of flowers, and may take just nectar and not also pollen from a flower, the collection from a particular flower of a bee that is carrying pollen does not necessarily mean that the pollen is from that flower. Microscopic examination of pollen on bees to identify the source of the pollen was beyond the scope of this study.

Female bees that collect much pollen from the flowers of a particular species of plant are often considered to be pollinating the flowers, but their true status as pollinators can be determined only by assessing the number of pollen grains deposited on stigmas. In contrast to female bees, male bees do not collect pollen to carry to nests, and they visit flowers comparatively fleetingly only to sup nectar and perhaps to feed on pollen grains. Compared to female bees, male bees are therefore far less likely to be effective pollinators.

Native plant names follow Jaffré et al. (2004), or the updated version of this checklist (Morat et al., 2012). Information presented here includes sources such as Donovan (1983), Pauly and Munzinger (2003), Nielsen et al. (2005), and Kato and Kawakita (2004).

Results

Forty-three species of native bees were identified from New Caledonia, and of these the females of 21 species visited the flowers of 116 native species of plants in 69 genera and 41 families (Tables 1 and 2). Twenty-one of these plant species belonged to the Myrtaceae, 10 to Dilleniaceae, nine to Cunoniaceae, seven each to Araliaceae and Fabaceae s.l. (including the Caesalpinioideae, Mimosoideae, and Papilionoideae), five each to Goodeniaceae and Proteaceae, and four each to Apocynaceae and Sapindaceae, while for the remaining families the number of species ranged from one to three. Species in Dilleniaceae and Myrtaceae were each visited by females of nine species of bees; Araliaceae by eight; Cunoniaceae and Ericaceae each by seven species; Goodeniaceae by six species; Arecaceae, Fabaceae, Proteaceae, and Violaceae each by five species; and the remaining families were visited by one to four species. Females of "6 + 1?" species of bees carried pollen from Dilleniaceae and Myrtaceae, six from Araliaceae, five from Goodeniaceae, "4 + 1?" from Cunoniaceae, four each from Fabaceae and Sapindaceae, and none to three from the remaining 34 families. Bees carried pollen from "64 + 4?" plant species, of which 11 belonged to Myrtaceae; six to Fabaceae; "5 + 2?" to Dilleniaceae; "4 + 1?" to Cunoniaceae; four to each of Araliaceae, Goodeniaceae, Proteaceae, and Sapindaceae; and none to two for the remaining families.

For introduced plants, female bees of 12 species visited 54 species in 43 genera and 19 families (Tables 1 and 2). Twelve of the plant species belonged to Asteraceae; eight to Fabaceae; seven to Verbenaceae; three each to Euphorbiaceae, Myrtaceae, and Solanaceae; and from one to two for the remaining families. Species in Fabaceae were visited by females of eight species of bees, Asteraceae and Verbenaceae by seven, Sapindaceae by four, and the remaining families by one to three. The females of seven species of bees visiting Fabaceae carried pollen, six carried pollen from Asteraceae, three carried pollen from each of Myrtaceae and Solanaceae, while none to "2 + 1?" carried pollen from the remaining families. Pollen was carried by female bees from six species of plants in both Asteraceae and Fabaceae, three in Solanaceae, and none to two in the remaining families.

One species each of Asteraceae and Convolvulaceae are of uncertain identity (Table 2) and were visited by females of three species of bees.

For species of bees with females that visited the flowers of native plants, of the six species with more than 10 records, *Austronomia sicheli* Vachal visited most species (53 spp.) and carried pollen from the highest number (29 spp.) (Table 3). However, for introduced plants only three species of bees visited 10 or more species, of which *Homalictus aponi* Cheesman & Perkins visited the most species (24 spp.) and carried pollen from the most species (14 spp.).

Discussion

Although the 43 native species of bees now known from New Caledonia are nearing double the mean of

Table 1. Alphabetic list of families, subfamilies, genera, and species of bees, bee voucher and bee collection data, and the vascular plants associated with each bee species.

Bee family, subfamily, tribe, genus, and species	Site of bee holotype and/or bee voucher information	Plant origin	Plant family
Colletidae			
Colletinae			
Leioproctus pacificus Michener (1965), subg. *Lamprocolletes* Smith	New Caledonia, Nepoui Valley, July 1940, *F. X. Williams, s.n.*, holotype ♂, BPBM	native native	Araliaceae Celastraceae
Leioproctus Smith, 1853, sp. indet. 2, aff. subg. *Lamprocolletes*	New Caledonia, Mt. Khogis (*sic*), 1 ♂, 1 Nov. 1992, *E. & M. Schlinger s.n.*, INHS		–
Hylaeinae			
Hylaeus Fabricius sp. indet. 1	New Caledonia, Ouen Toro Noumea, 1 ♀, 15 Jan. 1972, *P. Cochereau s.n.*, MNHNP		–
Hylaeus sp. indet. 2	New Caledonia, Port Laguerre, 1 ♀, 11 Apr. 2001, *J. Munzinger s.n.*, MNHNP		–
Hylaeus sp. indet. 3	New Caledonia, Forêt de Sailles, 1 ♀, 3 Dec. 2001, *J. Munzinger s.n.*, MNHNP		–
Palaeorhiza flavomellea Cockerell, 1910, subg. *Heterorhiza* Cockerell	Queensland, Australia, Cocotier Noumea, 1 ♀, 1 ♂, 27 May 1977, *A. Delobel s.n.*, MNHNP	native native native introduced introduced introduced	Arecaceae Elaeocarpaceae Hernandiaceae Anacardiaceae Combretaceae
Euryglossinae			
Euhesma Michener sp. indet. 1	New Caledonia, Mt. Koghi, 1 ♂, 4–6 Oct. 1967, *M. Sedlacek s.n.*, BPBM	native native native native native native	Cunoniaceae Dilleniaceae Myrtaceae Sapindaceae
Euryglossina Cockerell sp. indet. 1	New Caledonia, 1 ♀, 1 ♂, 3 July 1980, *G. McPherson s.n.*, BJD		
Euryglossina sp. indet. 2	New Caledonia, 2♀, Forêt de Sailles, 9 Dec. 2001, *J. Munzinger s.n.*, MNHNP		–
Halictidae			
Halictinae			
Homalictus aponi (Cheesman & Perkins, 1939)	Vanuatu, Malekula Island, St. Louis, 14 ♀, 1 ♂, 17 Aug. 1940, *F. X. Williams s.n.*, IRD	native native native native native native native native native	Araliaceae Asteraceae Cunoniaceae Dilleniaceae

Table 1. Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
Myodocarpus fraxinifolius Brongn. & Gris		–	♂ 1/2
Peripterygia marginata (Baill.) Loes.		♀ 1/1	–
–		–	–
–		–	–
–		–	–
–		–	–
Cocos nucifera L.		♀ 2/3	♂ 2/5
Elaeocarpus angustifolius Blume		–	♂ 1/1
Hernandia nymphaeifolia (C. Pres.) Kubitzki		–	♂ 5/5
Hernandia ovigera L.		–	♂ 1/5
Mangifera indica L.		–	♂ 1/3
Schinus terebinthifolia Raddi		–	♂ 3/10
Terminalia catappa L.		–	♂ 1/2
Codia albifrons (Brongn. ex Schinz & Guillaumin) Vieill. ex Guillaumin		♀ 1/2	–
Hibbertia heterotricha Bureau ex Guillaumin		♀ 1/1	–
Hibbertia pulchella (Brongn. & Gris) Schltr.		♀ 1/1	–
Hibbertia Andrews sp. indet.		♀ 1/5	–
Syzygium quadrangulare Guillaumin		♀ 1/5	–
Litchi chinensis Sonn.		♀ 1/1	♂ 1/1
–		–	–
Polyscias J. R. Forst. & G. Forst. sp. indet.		♀ 1/1 p	♂ 1/1
Blumea lacera (Burm. f.) DC.		♀ 1/1	–
Geissois Labill. sp. indet.		–	♂ 1/1
Pancheria billardierei (D. Don) Pamp.	*G. McPherson 3339*, MO	♀ 1/1 p	–
Hibbertia deplancheana Bureau ex Guillaumin		♀ 4/4 (2/2 p)	–
Hibbertia lucens Brong. & Gris. ex Sebert & Pancher	(1 ♀ p) *G. McPherson 3272*, MO; (3 ♀ p) *J. Munzinger 2527*, NOU	♀ 4/4 p	–
Hibbertia podocarpifolia Schltr.			
Hibbertia pulchella			
Hibbertia tontoutensis Guillaumin			
Hibbertia sp. indet.			

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
		native	Ericaceae (incl. Epacridaceae)
		native	Euphorbiaceae
		native	Fabaceae, Mimosoideae (= Mimosaceae)
		native	Goodeniaceae
		native	
		native	
		native	Loganiaceae
		native	Malpighiaceae
		native	Myrtaceae
		native	
		native	
		native	
		native	
		native	Onagraceae
		native	Orchidaceae
		native	Proteaceae
		native	Rubiaceae
		native	Sapotaceae
		native	Tiliaceae
		native	Violaceae
		introduced	Amaranthaceae
		introduced	Anacardiaceae
		introduced	Asteraceae
		introduced	
		introduced	
		introduced	
		introduced	
		introduced	
		introduced	
		introduced	Brassicaceae
		introduced	Euphorbiaceae
		introduced	
		introduced	Fabaceae, Caesalpinioideae (= Caesalpiniaceae)
		introduced	Fabaceae, Mimosoideae (= Mimosaceae)
		introduced	
		introduced	Malvaceae

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
Styphelia Sm. sp. indet., cf. *S. cymbulae* (Labill.) Spreng.		♀ 1/1	–
sp. indet.		♀ 1/1	♂ 1/4
Acacia spirorbis Labill.		♀ 4/13 (4/8 p)	♂ 1/1
Scaevola beckii Zahlbr.		♀ 2/2 p	–
Scaevola montana Labill.	(2 ♀ [1 ♀ p]) *G. McPherson 2966*, MO; (3 ♀ [2 ♀ p]) *G. McPherson 3254*, MO; (5 ♀ p) *G. McPherson 3260*, MO; (3 ♀ [1 ♀ p]) *G. McPherson 3281*, MO; (1 ♀ p) *G. McPherson 3779*, MO	♀ 9/18 (7/11 p)	♂ 1/1
Scaevola L. sp. indet.	*J. Munzinger 864*, NOU; *J. Munzinger 1382*, NOU; (2 ♀) *J. Munzinger 2958*, NOU	♀ 4/4 (1/1 p)	–
Geniostoma densiflora Baill.	*G. McPherson 3282*, MO	♀ 1/1	–
Acridocarpus austrocaledonicus Baill.	*J. C. Bradford 1053*, MO	♀ 1/1 p	–
Melaleuca quinquenervia (Cav.) S. T. Blake		♀ 2/5 p	–
Metrosideros operculata Labill. var. *operculata*	*G. McPherson 3786*, MO	♀ 1/1	–
Sannantha leratii (Schltr.) Peter G. Wilson [≡ *Babingtonia leratii* (Schltr.) A. R. Bean]		♀ 4/11 (1/2 p)	–
Sannantha virgata (J. R. Forst. & G. Forst.) Peter G. Wilson [≡ *Babingtonia virgata* (J. R. Forst. & G. Forst.) F. Muell.]	*J. Munzinger 2652*, NOU	♀ 1/1	–
Xanthostemon F. Muell. sp. indet.		–	♂ 1/1
Ludwigia octovalvis (Jacq.) P. H. Raven subsp. *octovalvis*	(2 ♀ p) *G. McPherson 3785*, MO	♀ 2/3 (1/2 p)	–
Eriaxis rigida Rchb. f.		♀ 1/1	–
Stenocarpus phyllodineus S. Moore	*G. McPherson 3317*, MO	♀ 1/1 p	–
Normandia neocaledonica Hook. f.		♀ 1/1	–
Leptostylis petiolata Vink		–	♂ 1/1
Corchorus L. sp. indet.		♀ 1/1	–
Agatea longipedicellata (Baker f.) Guillaumin & Thorne	*J. Munzinger 320*, NOU	♀ 1/1 (1/1 p)	–
Achyranthes aspera L.	*G. McPherson 3246*, MO	♀ 1/1	–
Schinus terebinthifolia		–	♂ 1/1
Bidens pilosa L.		♀ 1/1	♂ 1/1
Conyza Less. sp. indet., cf. *C. bonariensis* (L.) Cronquist		♀ 1/1	–
Calendula L. sp. indet.		♀ 1/1 p	–
Emilia sonchifolia (L.) DC.	(2 ♀ [1♀ p]) *G. McPherson 3267A*, MO	♀ 3/4 (1/1 p)	–
Tridax procumbens L.		♀ 3/13 (2/12 p)	–
Tridax L. sp. indet.		♀ 1/11 (1/6 p)	♂ 1/2
Youngia japonica (L.) DC.		♀ 1/1	–
Lepidium virginicum L.		♀ 1/1	–
Euphorbia hypericifolia L.		♀ 4/4 (3/4 p)	♂ 5/5
Euphorbia lophogona Lam.		♀ 1/1 p	–
Crotalaria L. sp. indet.	*J. Munzinger 445*, NOU	♀ 1/1	–
Leucaena leucocephala (Lam.) de Wit	(19 ♀ [15 ♀ p]) *G. McPherson 3237*, MO	♀ 4/30 (4/24 p)	–
Mimosa diplotricha C. Wright	(5 ♀ p) *G. McPherson 3776*, MO	♀ 2/6 p	–
Sida acuta Burm. f.		♀ 1/5 (1/4 p)	♂ 1/3

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
		introduced	
		introduced	Onagraceae
		introduced	Papaveraceae
		introduced	Solanaceae
		introduced	
		introduced	
		introduced	Verbenaceae
		introduced	
		introduced	
		introduced	Zygophyllaceae
Homalictus cocos Pauly & Munzinger, 2003	New Caledonia, St. Louis, 1 ♀, 17 Aug. 1940, *F. X. Williams s.n.*, IRD	native	Araliaceae
		native	Arecaceae
		introduced	Anacardiaceae
			Euphorbiaceae
			Verbenaceae
Homalictus risbeci (Cockerell, 1929)	New Caledonia, Nepoui Valley, 10 ♀, July 1940, *F. X. Williams s.n.*, IRD	native	Araliaceae
		native	
		native	
		native	Asteraceae
		native	Cunoniaceae
		native	
		native	
		native	
		native	
		native	
		native	Dilleniaceae
		native	
		native	
		native	
		native	Ericaceae (incl. Epacridaceae)
		native	Fabaceae, Mimosoideae (= Mimosaceae)
		native	Goodeniaceae
		native	
		native	
		native	
		native	Laxmanniaceae (treated as Agavaceae in Jaffré et al., 2001, 2004)
		native	Liliaceae
		native	Linaceae
		native	Malpighiaceae
		native	Malvaceae
		native	Melastomataceae
		native	Myrtaceae
		native	
		native	
		native	
		native	
		native	
		native	Onagraceae
		native	Proteaceae
		native	

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
Sida rhombifolia L.		♀ 7/7	–
Bougainvillea Comm. ex Juss. sp. indet.		–	♂ 1/1
Argemone mexicana L.	*G. McPherson 3255*, MO	♀ 2/16 (2/9 p)	–
Solanum lycopersicum L.	*J. Munzinger 609*, NOU	♀ 2/2 (1/1 p)	–
Solanum torvum Sw.		♀ 1/9 (1/6 p)	–
Solanum L. sp. indet.		♀ 1/1	–
Duranta repens L.		♀ 1/1	♂ 1/1
Stachytarpheta indica (L.) Vahl		♀ 1/1	♂ 1/8
Verbena L. sp. indet.		♀ 1/11 (1/7 p)	♂ 1/1
Tribulus cistoides L.		♀ 9/15 (6/12 p)	♂ 1/1
Meryta J. R. Forst. & G. Forst. sp. indet.		♀ 1/1	–
Cocos nucifera		♀ 2/2	–
Schinus terebinthifolia		♀ 2/3 (2/2 p)	♂ 2/12
Poinsettia Graham sp. indet.		♀ 3/3	♂ 1/1
Verbena sp. indet.		♀ 1/1	–
Polyscias sessiliflora Marais subsp. indet.		–	♂ 1/1
Polyscias sp. indet.		♀ 2/6 (2/5 p)	♂ 2/9
genus and sp. indet.		–	♂ 1/1
Blumea lacera		♀ 1/1	–
Geissois sp. indet.		–	♂ 1/1
Pancheria alaternoides Brongn. & Gris	*J. Munzinger 2818*, NOU	♀ 1/1	–
Pancheria billardierei		♀ 1/1	–
Pancheria phylliraeoides Brongn. & Gris ex Guillaumin	*G. McPherson 3339*, MO	♀ 1/6 p	–
Pancheria Brongn. & Gris sp. indet.		–	♂ 1/1
Hibbertia lucens	(2 ♀) *G. McPherson 3272*, MO; (1 ♀) *J. Munzinger 959*, NOU	♀ 2/3 p	–
Hibbertia pancheri (Brongn. & Gris) Briq.		♀ 1/1	–
Hibbertia sp. indet.		♀ 1/1	–
Dracophyllum verticillatum Labill.	*J. Munzinger 2957*, NOU	♀ 0/2	♂ 4/4
Acacia spirorbis		♀ 1/2 p	–
Scaevola beckii		♀ 1/1	–
Scaevola cylindrica Schltr. & K. Krause		–	♂ 1/2
Scaevola montana	(1 ♂) *G. McPherson 3260*; (1 ♀, 1♂) *G. McPherson 3779*, MO	♀ 1/1	♂ 3/3
Scaevola sp. indet.		♀ 1/1	–
Cordyline Comm. ex R. Br. sp. indet.		–	♂ 2/2
Rhuacophila javanica Blume	*J. Munzinger 3046*, NOU	♀ 1/1	–
Hugonia penicillanthemum Baill. ex Pancher & Sebert	*G. McPherson 3270*, MO	♀ 1/1 p	–
Tristellateia australasiae A. Rich.		♀ 1/1 p	–
Melochia odorata L. f.	*G. McPherson 3267*, MO	♀ 2/5 (1/2 p)	♂ 2/3
Melastoma malabathricum L. subsp. *malabathricum*		♀ 4/4	♂ 1/1
Cloezia floribunda Brongn. & Gris		–	♂ 2/2
Melaleuca quinquenervia		♀ 4/11 (3/10 p)	♂ 3/36
Metrosideros operculata	*G. McPherson 3786*, MO	♀ 1/3 p	–
Sannantha leratii		♀ 3/3 (1/1 p)	♂ 13/24
Syzygium P. Browne ex Gaertn. sp. indet.		♀ 1/2 (1/1 p)	♂ 1/1
Tristaniopsis calobuxus Brongn. & Gris		♀ 1/1 p	♂ 1/1
Ludwigia octovalvis subsp. *octovalvis*	*G. McPherson 3785*, MO	♀ 2/2	♂ 1/1
Grevillea R. Br. ex Knight sp. indet.		–	♂ 1/1
Stenocarpus phyllodineus	*G. McPherson 3317*, MO	♀ 1/2	♂ 1/1

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
		native	Rhizophoraceae
		native	Rubiaceae
		native	Sapindaceae
		native	
		native	Surianaceae
		introduced	Asteraceae
		introduced	Brassicaceae
		introduced	Fabaceae, Caesalpinioideae (= Caesalpiniaceae)
		introduced	Fabaceae, Mimosoideae (= Mimosaceae)
		introduced	
		introduced	Fabaceae, Papilionoideae
		introduced	Lythraceae
		introduced	Rutaceae
		introduced	Verbenaceae
Homalictus Cockerell sp. indet. 4	New Caledonia, Mt. Panie Trail, 3 ♀, 2 ♂, 8–9 Feb. 1963, *C. M. Yoshimoto s.n.*, IRD	native	Cunoniaceae
		native	Dilleniaceae
		native	
		native	Ericaceae (incl. Epacridaceae)
		native	
		native	Goodeniaceae
		native	Loganiaceae
		native	Myrtaceae
		native	
		native	Rubiaceae
		native	
		native	Rutaceae
		native or introduced	Asteraceae
Homalictus sp. indet. 5	New Caledonia, Hienghene, 2 ♀, 25 Nov. 1958, *C. R. Joyce s.n.*, IRD		–
Homalictus sp. indet. 6	New Caledonia, Mou, 3 ♀, 25 Dec. 1979, *B. J. Donovan s.n.*, BJD; Houailou, near tower, 1 ♂, 25 Dec. 1979, *G. McPherson s.n.*, BJD	native	Arecaceae
		native	Boraginaceae
		native	Myrtaceae
Homalictus sp. indet. 7	New Caledonia, Mts. des Koghis, 3 ♂, Jan. 1969, *N. L. H. Krauss s.n.*, BPBM		–
Homalictus sp. indet. 8	New Caledonia, Thi River Valley, 1 ♀, 6 Nov. 1940, *F. X. Williams s.n.*, IRD	native	Araliaceae
		native	
		native	Myodocarpaceae
		native	Rhamnaceae
		native	Sapindaceae
		introduced	Asteraceae
		introduced	Sapindaceae
Homalictus sp. indet. 9	New Caledonia, Mt. Koghi, 1 ♀, Dec. 1963, *R. Straatman s.n.*, BPBM	native	Araliaceae
			Arecaceae
			Cunoniaceae
			Myrtaceae

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
Rhizophora apiculata Blume	*J. Munzinger 2959*, NOU	♀ 1/1	–
Normandia neocaledonica		♀ 1/1 p	–
Cupaniopsis myrmoctona Radlk.	*J. Munzinger 4219*, NOU	♀ 1/1 p	–
Guioa villosa Radlk.		♀ 2/3 p	–
Suriana maritima L.	*G. McPherson 3245*, MO	♀ 1/1	–
Cosmos sulphureus Cav.		♀ 1/1	–
Brassica L. sp. indet.		♀ 2/4 (1/2 p)	–
Cassia fistula L.		♀ 1/1 p	–
Leucaena leucocephala		♀ 7/21 (7/20 p)	–
Mimosa diplotricha	*G. McPherson 3776*, MO	♀ 1/1 p	–
Crotalaria L. sp. indet.		♀ 1/1	–
Lagerstroemia indica L.		♀ 1/1	–
Citrus L. sp. indet.		♀ 1/8 p	–
Stachytarpheta Vahl sp. indet.		♀ 1/1	–
Pancheria robusta Guillaumin	*G. McPherson 3277D*, MO	♀ 2/4 p	–
Hibbertia lucens	*J. Munzinger 959*, NOU	♀ 2/2 (1/2 p)	–
Hibbertia trachyphylla Schltr.		–	♂ 1/3
Dracophyllum involucratum Brongn. & Gris		♀ 1/1 p	–
Scaevola beckii		♀ 1/1 p	–
Geniostoma densiflorum	*G. McPherson 3268*, MO	♀ 1/1 p	–
Metrosideros operculata var. *francii* J. W. Dawson		♀ 1/1	–
Metrosideros punctata J. W. Dawson		♀ 1/1 p	–
Normandia neocaledonica		♀ 1/1 p	–
Psychotria rupicola (Baill.) Schltr.	*G. McPherson 3277A*, MO	♀ 1/3 p	–
Zanthoxylum L. sp. indet.	*J. Munzinger 2567*, NOU	–	♂ 1/1
sp. indet.		♀ 1/1	–
–		–	–
Cocos nucifera		♀ 1/3 p	–
Heliotropium foertherianum Diane & Hilger		♀ 1/1	–
Sannantha leratii		–	♂ 1/1
–			
Polyscias sessiliflora subsp. indet.		♀ 1/1 p	–
Polyscias sp. indet.		♀ 1/5 p	–
Myodocarpus Brongn. & Gris sp. indet.	*P. Lowry 6509*, MO	♀ 1/1	–
Alphitonia neocaledonica (Schltr.) Guillaumin	*J. Munzinger 2006*, NOU	♀ 4/4	–
Guioa villosa		♀ 1/1 p	–
Ageratum L. sp. indet.		♀ 1/1 p	–
Litchi chinensis		♀ 2/3	–
Polyscias sessiliflora subsp. indet.		♀ 1/4 p	–
Schefflera vieillardii Baill.		♀ 1/1	–
Cyphokentia cerifera (H. E. Moore) Pintaud & W. J. Baker		♀ 1/1	–
Cunonia balansae Brongn. & Gris	*J. Munzinger 2520*, NOU	♀ 1/1	–
Geissois racemosa Labill.	*J. Munzinger 2680*, NOU	♀ 1/1	–
Metrosideros Banks ex Gaertn. sp. indet.		♀ 1/6 p	–

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
Homalictus sp. indet. 10	New Caledonia, Col de Roussettes, 1 ♀, 4–6 Feb. 1963, *G. Kuschel s.n.*, BPBM		–
Homalictus sp. indet. 11	New Caledonia, Île.Mouac, 1 ♂, 19 Oct. 1958, *C. R. Joyce s.n.*, IRD		–
Lasioglossum polygoni (Cockerell, 1929), subsp. indet. 1, subg. *Chilalictus*	New Caledonia, Col d'Amieu, 21 July 1977, *A. Delobeli s.n.*, ♀ holotype and 2 ♀ paratypes, MNHNP	native	Araliaceae
		native	Arecaceae
		native	Cunoniaceae
		native	Dilleniaceae
		native	Ericaceae (incl. Epacridaceae)
		native	Melastomataceae
		native	Myrtaceae
		native	Phellinaceae
		introduced	Sapindaceae
		introduced	Verbenaceae
Lasioglossum polygoni subsp. indet. 2, subg. *Chilalictus*	New Caledonia, Haute-Ni, 1 ♀, 23 Oct. 2004, *J. Munzinger s.n.*, MNHNP	native	Araliaceae
		native	
		native	Cunoniaceae
		native	Dilleniaceae
		native	Elaeocarpaceae
		native	
		native	Ericaceae (incl. Epacridaceae)
		native	Goodeniaceae
		native	Myrtaceae
		native	Sapindaceae
		native	
		native	
		introduced	Asteraceae
		introduced	Fabaceae, Mimosoideae (= Mimosaceae)
		introduced	Sapindaceae
Lasioglossum polygoni subsp. indet. 3, subg. *Chilalictus*	New Caledonia, Bourail, 27 May 1927, *T. D. A. Cockerell s.n.*, 1 ♀ holotype, MNHNP	native	Asteraceae
		native	Elaeocarpaceae
		native	Violaceae
		introduced	Malvaceae
			Polygonaceae
			Solanaceae
Lasioglossum Curtis sp. indet. 4, subg. *Chilalictus*	New Caledonia, Forêt de Sailles, 1 ♀, 9 Dec. 2001, *J. Munzinger s.n.*, MNHNP	native	Apocynaceae
			Araliaceae
			Dilleniaceae
			Ericaceae (incl. Epacridaceae)
			Liliaceae
			Phellinaceae
Lasioglossum sp. indet. 5, subg. *Chilalictus*	New Caledonia, Mt. Khogis, 22 Dec. 1992, *M. E. Irwin & D. W. Webb s.n.*, INHS-96,625 (1 ♀), INHS-96,607 (1 ♂)		–

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
–		–	–
–		–	–
Polyscias dioica (Vieill. ex Pancher & Sebert) Harms	*J. Munzinger 1732*, NOU	♀ 3/3	–
Cyphokentia cerifera		♀ 2/2	–
Geissois racemosa	*J. Munzinger 2680*, NOU	♀ 4/4	–
Hibbertia lucens	(1 ♀) *J. Munzinger 959*, NOU	♀ 2/2	–
Dracophyllum ramosum Pancher ex Brongn. & Gris	*J. Munzinger 2043*, NOU	–	♂ 1/1
Melastoma malabathricum subsp. *malabathricum*		♀ 13/13 (1/14 p)	–
Myrtastrum rufopunctatum (Pancher ex Brongn. & Gris) Burret		♀ 1/1	–
Phelline lucida Vieill. ex Baill.	*J. Munzinger 2502*, NOU	♀ 2/2	–
Litchi chinensis		♀ 1/1 p	–
Lantana L. sp. indet		♀ 1/3	–
Polyscias dioica	*J. Munzinger 1732*, NOU	♀ 1/1	–
Polyscias sessiliflora subsp. indet.		♀ 1/2 p	–
Polyscias sp. indet.		♀ 3/12 (3/11 p)	–
Pancheria sebertii Guillaumin		♀ 1/1	–
Hibbertia nana Däniker		♀ 1/1	–
Elaeocarpus dognyensis Guillaumin		♀ 1/1	–
Elaeocarpus speciosus Brongn. & Gris.	*J. Munzinger 3058*, NOU	♀ 2/2	–
Styphelia cf. *cymbulae* Spreng.	*J. Munzinger 2495*, NOU	♀ 1/1	–
Scaevola beckii		♀ 2/3 (1/1 p)	–
Syzygium quadrangulare		♀ 1/2 p	–
Cupaniopsis oedipoda Radlk.	*G. McPherson 3227*, MO	♀ 1/1 p	–
Cupaniopsis Radlk. sp. indet.	*G. McPherson 2744*, MO	♀ 1/2 p	–
Guioa villosa	*G. McPherson 3238*, MO	♀ 1/1 p	–
Ageratum conyzoides L.		♀ 4/19 p	–
Leucaena leucocephala	*G. McPherson 3237*, MO	♀ 1/1 p	–
Litchi chinensis		♀ 3/9 (1/3 p)	–
Blumea lacera		♀ 1/2 (1/1 p)	–
Elaeocarpus angustifolius		–	♂ 1/1
Agatea longipedicellata	*J. Munzinger 396*, NOU	♀ 1/1	–
Sida acuta		♀ 1/22 (1/20 p)	–
Antigonon leptopus Hook. & Arn.		♀ 2/2	–
Polygonum L. sp. indet.		♀ 1/1	–
Solanum torvum		♀ 1/4 (1/3 p)	–
Parsonsia R. Br. sp. indet.	*J. Munzinger 4051*, NOU	–	♂ 1/1
Polyscias dioica	*J. Munzinger 1732*, NOU	♀ 2/2	–
Hibbertia nana	*J. Munzinger 1649*, NOU	♀ 2/2	–
Dracophyllum involucratum	*F. Tronchet 609*, NOU	♀ 3/3	–
Rhuacophila javanica	*Th. Le Borgne 39*, NOU	♀ 3/3	–
Phelline lucida	*J. Munzinger 2502*, NOU	♀ 1/1	–
–		–	–

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
Lasioglossum sp. indet. 6, subg. *Chilalictus*	New Caledonia, Upper Vallée La Ni, 2 ♀, 2 Nov. 1992, *M. E. Irwin & D. W. Webb s.n.*, INHS-96,626, INHS-96,627		–
Lasioglossum sp. indet. 7, subg. *Chilalictus*	New Caledonia, Vallée de la Tchamba, 1 ♀, 26 July 2005, *J. Munzinger s.n.*, MNHNP	native	Melastomataceae
Lasioglossum sp. indet. 8, subg. *Chilalictus*	New Caledonia, Ni Valle, 1 ♀, 2 Nov. 1992, *M. E. Irwin & D. W. Webb s.n.*, INHS-96,642		–
Lasioglossum sp. indet. 9, from an undescribed subgenus	New Caledonia, Haute-Ni, 1 ♀, 23 Oct. 2004, *J. Munzinger s.n.*, MNHNP	native	Ericaceae (incl. Epacridaceae)
Lasioglossum sulthicum (Smith, 1853), subg. *Parasphecodes* Smith	Australia, Mt. Kogis, 1 ♀, 30 Oct. 1992, *M. E. Irwin & D. W. Webb s.n.*, INHS-96,695		–
Nomiinae			
Austronomia cheesmanae (Michener, 1965)	New Caledonia, Lifu, Cape des Pins, 18 Nov. 1950, *L. E. Cheesman s.n.* (1 ♀), holotype, BMNH	native	Myoporaceae
Austronomia sicheli (Vachal, 1897)	New Caledonia, 1 ♀, s.d., *J. Sichel s.n.*, MNHNP	native	Apocynaceae
		native	Araliaceae
		native	
		native	
		native	Celastraceae
		native	Combretaceae
		native	Connaraceae
		native	Cunoniaceae
		native	Dilleniaceae
		native	
		native	
		native	
		native	
		native	Ericaceae (incl. Epacridaceae)
		native	
		native	
		native	Escalloniaceae
		native	Fabaceae, Caesalpinioideae
		native	
		native	
		native	
		native	Fabaceae, Mimosoideae (= Mimosaceae)
		native	Goodeniaceae
		native	
		native	
		native	
		native	Joinvilleaceae

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
–		–	–
Melastoma malabathricum subsp. *malabathricum*		♀ 1/1	♂ 1/1
–		–	–
Styphelia cf. *cymbulae*	*J. Munzinger 2495*, NOU	♀ 1/1	–
–		–	–
Myoporum crassifolium G. Forst.		♀1/1	–
Parsonsia crebriflora Baill.	*J. Munzinger 1733*, NOU	♀ 6/6	–
Polyscias sessiliflora subsp. indet.		♀ 1/5 p	–
Polyscias sp. indet.		♀ 1/5 (1/3 p)	–
sp. indet. 1		♀ 1/2	–
Peripterygia marginata	*G. McPherson 3284*, MO	♀ 1/1	–
Lumnitzera racemosa Willd.	*J. Munzinger 2668*, NOU	–	♂ 2/2
sp. indet. 1		♀ 2/3 p	–
Codia discolor (Brongn. & Gris) Guillaumin	*J. Munzinger 2651*, NOU	♀ 2/2 p	–
Hibbertia bouletii Veillon		?1/1	?1/1
Hibbertia lucens	(4 ♀ p) *G. McPherson 3272*, MO; (4 ♀) *J. Munzinger 959*; (1 ♀) *J. Munzinger 2527*, NOU	♀ 6/9 (6/6 p)	–
Hibbertia pancheri		♀ 1/1	–
Hibbertia pulchella		♀ 2/2	–
Hibbertia sp. indet.	(2 ♀ p) *J. C. Bradford 1116*, MO	♀ 3/9 (3/7 p)	–
Dracophyllum verticillatum		♀ 0/1	–
Styphelia pancheri (Brongn. & Gris) F. Muell.	*J. Munzinger 395*, NOU	♀ 1/1	–
Styphelia cf. *cymbulae*	*J. Munzinger 2495*, NOU	♀ 2/2	–
Argophyllum montanum Schltr.	*G. McPherson 3269*, MO	♀ 1/1 p	–
Cassia fistula		♀ 1/3 p	–
Cassia L. sp. indet.		♀ 3/4 (3/3 p)	–
Storckiella pancheri Baill.		♀ 1/1 p	–
Storckiella Seem. sp. indet.		♀ 2/4 (2/3 p)	–
Acacia spirorbis		♀ 2/2 p	♂ 1/1
Scaevola beckii		♀ 2/3 (1/1 p)	–
Scaevola cylindrica	(1♀, 1♂) *G. McPherson 2300*, MO	♀ 2/2	♂ 2/3
Scaevola erosa Guillaumin ex I. H. Müll.		♀ 1/1	–
Scaevola montana	(1 ♀) *G. McPherson 3260*, MO; (9 ♀) *G. McPherson 3281*, MO; (1 ♂) *G. McPherson 3779*, MO; (1 ♀) *J. Munzinger 4725*, NOU	♀ 5/12	♂ 2/2
Joinvillea Gaudich. ex Brongn. & Gris sp. indet.		♀ 1/2 p	–

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
		native	Loganiaceae
		native	Malpighiaceae
		native	Melastomataceae
		native	
		native	Myodocarpaceae
		native	Myrsinaceae
		native	Myrtaceae
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	
		native	Proteaceae
		native	
		native	
		native	
		native	Rhamnaceae
		native	Rubiaceae
		native	Sapindaceae
		native	
		native	Violaceae
		introduced	Anacardiaceae
		introduced	Asteraceae
		introduced	Euphorbiaceae
		introduced	Fabaceae, Mimosoideae (= Mimosaceae)
		introduced	
		introduced	Fabaceae, Papilionoideae
		introduced	Lamiaceae
		introduced	Myrtaceae
		introduced	
		introduced	Phrymaceae
		introduced	Sapindaceae
		introduced	Solanaceae
		introduced	
		introduced	Verbenaceae
		native or introduced	Convolvulaceae
Austronomia (L.) Link sp. indet. 3	New Caledonia, Mt. Do, 1 ♀, 15 Dec. 2000, *B. J. Donovan s.n.*, BJD	introduced	Fabaceae, Papilionoideae
Austronomia sp. indet. 4	New Caledonia, Loyalty Islands, Lifu Island, 1 ♀, 26–27 Mar. 1968, *J. L. Gressit & T. C. Maa s.n.*, BPBM		–

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
Geniostoma densiflorum	*G. McPherson 3282*, MO	♀ 1/3	–
Tristellateia australasiae		♀ 1/1	–
Melastoma denticulatum Labill.		♀ 2/5 (1/3 p)	–
Melastoma malabathricum subsp. *malabathricum*		♀ 4/5 (1/2 p)	–
Myodocarpus fraxinifolius		♀ 2/1 (2/2 p)	♂ 1/3
Tapeinosperma oblongifolium Mez	*J. Munzinger 1954*, NOU		
Cloezia artensis (Montrouz.) P. S. Green	(3 ♀, 4 ♂) *G. McPherson 3258*, MO	♀ 1/3	♂ 3/5
Cloezia Brongn. & Gris sp. indet.		♀ 1/4	♂ 1/1
Melaleuca gnidioides Brongn. & Gris		♀ 1/2 p	–
Melaleuca quinquenervia		♀ 3/4 (2/3 p)	♂ 3/8
Myrtastrum rufopunctatum		♀ 1/1	–
Myrtus L. sp. indet.		–	♂ 1/73
Sannantha leratii		♀ 9/14	♂ 3/17
Sannantha Peter G. Wilson sp. indet.	*J. Munzinger 456*, NOU	–	♂ 1/1
Syzygium lateriflorum Brongn. & Gris		♀ 3/12 (1/3 p)	♂ 1/1
Syzygium quadrangulare		♀ 1/2 (1/1 p)	–
Tristaniopsis calobuxus		♀ 2/5	♂ 3/10
Tristaniopsis glauca Brongn. & Gris		♀ 1/1	–
Tristaniopsis vieillardii Brongn. & Gris	*J. Munzinger 4679*, NOU	♀ 1/1	–
Uromyrtus emarginata (Panch. ex Brongn. & Gris) Burret	*J. Munzinger 394*, NOU	♀ 1/1	–
sp. indet. 1		♀ 1/1 p	–
sp. indet. 2	*J. C. Bradford 1115*, MO	♀ 1/2 p	–
Grevillea exul Lindl.	*G. McPherson 3271*, MO	♀ 2/8 (2/4 p)	–
Stenocarpus milnei Hook.	*G. McPherson 3285*, MO	♀ 2/14 (1/1 p)	♂ 2/4
Stenocarpus umbelliferus Druce		♀ 1/1	–
Stenocarpus R. Br. sp. indet.		♀ 1/1 p	♂ 1/6
Alphitonia neocaledonica	*J. Munzinger 2006*, NOU	♀ 1/1	–
Normandia neocaledonica	*G. McPherson 3221*, MO	♀ 1/1 p	–
Guioa villosa		♀ 2/2 p	–
Storthocalyx pancheri (Baill.) Radlk.	*J. Munzinger 2053*, NOU	? 1/1	? 1/1
Agatea longipedicellata	*J. Munzinger 320*, NOU	♀ 20/20 p	♂ 11/11
Schinus terebinthifolia	(3 ♀ [1 ♀ p]) *G. McPherson 3241*, MO	♀ 5/9 (3/3 p)	♂ 1/8
Ageratum conyzoides		♀ 3/17 (3/13 p)	–
Poinsettia sp. indet.		♀ 2/2	♂ 1/1
Leucaena leucocephala		♀ 5/12 p	–
Mimosa diplotricha	*G. McPherson 3776*, MO	♀ 1/1	–
Senna occidentalis (L.) Link		♀ 1/1 p	–
Mentha L. sp. indet.		♀ 1/2	–
Psidium guajava L.		♀ 1/8 (1/5 p)	–
Syzygium jambolanum (Lam.) DC.		♀ 1/2	–
Mimulus L. sp. indet.		♀ 1/1	–
Litchi chinensis		♀ 1/1	–
Solanum torvum	(1 ♀ p) *G. McPherson 3766B*, MO	♀ 3/12 p	–
sp. indet. 1		♀ 2/13 p	–
Stachytarpheta indica		♀ 1/1	–
Ipomoea L. sp. indet.		♀ 1/2 p	–
Senna occidentalis		♀ 1/1	–
–		–	–

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
Austronomia sp. indet. 5	New Caledonia, Mt. Koghis, 1 ♂, 22 Dec. 1992, *M. Irwin & D. W. Webb s.n.*, INHS		–
Megachilidae			
Megachilinae			
Lithurgini			
Lithurgus scabrosus (Smith, 1859), subg. *Lithurgus* Berthold	Ile Aru, Indonesia, Noumea, 1 ♂, July 1900, *J. J. Walker s.n.*, MNHNP	native native or introduced	Convolvulaceae Convolvulaceae
Megachilini			
Megachile laticeps Smith, 1853, subg. *Aethomegachile* Engel & Baker	Iles Phillipines, Noumea, 1 ♀, July 1957, *J. Rageau s.n.*, MNHNP	native native introduced	Convolvulaceae Myrtaceae Verbenaceae
Megachile rambutwan Cheesman, 1936, subg. *Callomegachile* Michener	Vanuatu, Noumea, 1 ♂, Aug. 1900, *J. J. Walker s.n.*, MNHNP		
Megachile umbripenne Smith, 1853, subg. *Callomegachile*	Nepal, Noumea, 2 ♀, 15 Oct. 1980, *B. J. Donovan s.n.*, BJD	native introduced introduced introduced introduced	Proteaceae Asteraceae Fabaceae, Papilionoideae Polygonaceae Verbenaceae
Megachile albomarginata Smith, 1879, subg. *Eutricharaea* Thomson	New Caledonia, Mt. Mou, 1 ♀, 12 Mar. 1914, *P. D. Montague 541*, MNHN	native native native native native native native native native native native native native native native introduced introduced introduced introduced introduced introduced introduced introduced introduced introduced introduced introduced introduced	Apocynaceae Araliaceae Connaraceae Dilleniaceae Goodeniaceae Myrtaceae Proteaceae Violaceae Asteraceae Fabaceae, Mimosoideae (= Mimosaceae) Lamiaceae Myrtaceae Tiliaceae Verbenaceae

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
–		–	–
Ipomoea pes-caprae (L.) R. Br.		♀ 2/2	♂ 2/2
Ipomoea sp. indet.		♀ 2/4 (1/2 p)	♂ 1/8
Ipomoea pes-caprae		♀ 1/1	♂ 1/7
Sannantha pinifolia (Labill.) Peter G. Wilson [≡ *Babingtonia pinifolia* (Labill.) A. R. Bean]		♀ 0/1	–
Duranta repens		–	♂ 0/2
–	–	–	–
Stenocarpus sp. indet.		♀ 1/7 (1/4 p)	♂ 1/3
Bidens pilosa		–	♂ 2/8
Cytisus cajan L.	*G. McPherson 3240*, MO	♀ 1/2 (1/1 p)	–
Antigonon leptopus		–	♂ 3/3
Duranta repens		–	♂ 2/2
Parsonsia crebriflora	*J. Munzinger 1733*, NOU	♀ 1/1 p	–
Rauwolfia semperflorens (Müll. Arg.) Schltr.	*G. McPherson 3235*, MO	♀ 1/1	♂ 1/2
sp. indet.		♀ 1/1 p	–
Tieghemopanax R. Vig. sp. indet.	*G. McPherson 3787*, MO	♀ 1/1 p	–
sp. indet. 1		♀ 1/1 p	–
Hibbertia podocarpifolia		♀ 1/2 p	–
Hibbertia lucens	(2 ♀) *J. Munzinger 959*, NOU; (1 ♀) *J. Munzinger 2527*, NOU	♀ 4/5 (2/5 p)	–
Hibbertia sp. indet.		♀ 1/1	–
Scaevola beckii		♀ 1/1 p	–
Scaevola erosa		♀ 2/2 (1/1 p)	–
Scaevola montana	(2 ♂) *G. McPherson 3236*, MO; (1 ♀ 3 ♂) *G. McPherson 3779*, MO	♀ 1/1 p	♂ 3/5
Syzygium lateriflorum		–	♂ 1/1
Stenocarpus sp. indet.		♀ 1/1	-
Agatea longipedicellata	*J. Munzinger 320, 396*, NOU	♀ 8/8	♂ 1/1
Agatea rufotomentosa (Baker f.) J. Munzinger	*J. Munzinger 370, 371*, NOU	♀ 2/2 (1/2 p)	–
Ageratum sp. indet.		♀ 2/2 (1/1 p)	–
Bidens L. sp. indet.		–	♂ 1/1
Cosmos Cav. sp. indet.		♀ 1/3	-
Tridax procumbens		–	♂ 1/1
Albizia Durazz. sp. indet.		♀ 1/6 (1/5 p)	–
Leucaena leucocephala	(1 ♀ p) *G. McPherson 3237*, MO	♀ 2/4 p	–
Mimosa diplotricha	*G. McPherson 3776*, MO	♀ 1/1 p	–
Ocimum gratissimum L.	*G. McPherson 3267C*, MO	♀ 1/1 p	–
Psidium guajava		♀ 1/1 p	–
Callistemon R. Br. sp. indet.		♀ 0/1	–
Triumfetta rhomboidea Jacq.		♀ 1/1 p	–
Duranta repens		–	♂ 1/1
Stachytarpheta indica	(3 ♀ [1 ♀ p] 2 ♂) *G. McPherson 3249*, MO	♀ 2/4 (1/1 p)	♂ 5/8

Table 1. Continued.

Bee family, subfamily, tribe, genus, and species	Insect voucher information	Plant origin	Plant family
Megachile australasiae Dalla Torre, 1896, subg. *Eutricharaea*	Australia, species not seen		–
Megachile australis Lucas, 1876, subg. *Eutricharaea*	New Caledonia, Noumea, 1 ♀, June 1900, *J. J. Walker s.n.*, MNHNP	native	Aizoaceae
		native	Apocynaceae
		native	
		native	Asteraceae
		native	Convolvulaceae
		native	Dilleniaceae
		native	Euphorbiaceae
		native	Fabaceae, Papilionoideae
		native	Goodeniaceae
		native	Labiatae
		native	Myrtaceae
		native	
		native	
		native	Onagraceae
		native	Santalaceae
		native	Surianaceae
		introduced	Amaranthaceae
		introduced	Asteraceae
		introduced	
		introduced	
		introduced	
		introduced	
		introduced	Euphorbiaceae
		introduced	Fabaceae, Mimosoideae (= Mimosaceae)
		introduced	
		introduced	Myrtaceae
		introduced	Poaceae
		introduced	Tiliaceae
		introduced	Verbenaceae
		introduced	Zygophyllaceae
Megachile fullawayi Cockerell, 1914, subg. *Eutricharaea*	Guam, Noumea, 1 ♂, July 1914, *F. X. Williams s.n.*, MNHNP		–
Megachile aurantiaca Friese, 1905, subg. *Hackeriapis* Cockerell	New Caledonia, Dumbea, 1 ♂, 19 Dec. 1979, *B. J. Donovan s.n.*, BJD	native	Apocynaceae
		native	Fabaceae, Papilionoideae
		native	Flacourtiaceae
		native	Liliaceae
		native	Violaceae
Apidae			
Xylocopinae			
Ceratina dentipes Friese, 1914, subg. *Neoceratina* Perkins	Java, Buitenzorg, 16 km SE La Foa, 1 ♀, 20–22 Dec. 1991, *M. E. Irwin, D. W. Webb s.n.*, INHS-22,419	introduced	Verbenaceae

Table 1. Continued, Extended.

Plant species	Plant voucher information	Bee collection data ♀	Bee collection data ♂
–		–	–
Sesuvium portulacastrum L.		♀ 1/1	–
Melodinus J. R. Forst. & G. Forst. sp. indet.		♀ 1/1	–
Rauwolfia semperflorens	*G. McPherson 3235*, MO	–	♂ 1/1
Tridax procumbens		♀ 6/10 (2/3 p)	♂ 1/1
Ipomoea pes-caprae		–	♂ 2/2
Tetracera billardieri Martelli	*J. Munzinger 861*, NOU	♀ 1/1 p	♂ 1/1
Cleistanthus stipitatus (Baill.) Müll. Arg.		♀ 1/1	–
Desmodium incanum DC.	*J. C. Bradford 1074*, MO	♀ 1/1 p	–
Scaevola sericea Vahl		–	♂ 1/1
Premna serratifolia L.		♀ 1/1	–
Melaleuca quinquenervia		♀ 1/1	–
Metrosideros operculata	*G. McPherson 3786*, MO	–	♂ 1/1
Sannantha sp. indet. (sensu *Babingtonia*)		♀ 1/1	–
Ludwigia octovalvis subsp. *octovalvis*	(3 ♀ [1 ♀ p] 1 ♂) *G. McPherson 3785*, MO	♀ 1/3 (1/1 p)	♂ 3/3
Santalum austrocaledonicum Vieill.	*J. Munzinger 4518*, NOU	–	♂ 1/1
Suriana maritima	*G. McPherson 3245*, MO	–	♂ 2/4
Achyranthes aspera	*G. McPherson 3246*, MO	♀ 1/1	♂ 1/2
Bidens sp. indet.		♀ 1/1	–
Cosmos sulphureus		♀ 1/1	♂ 1/1
Cosmos sp. indet.		♀ 1/3	♂ 1/1
Sphagneticola trilobata (L.) Pruski	*J. Munzinger 405*, NOU	–	♂ 2/2
Tridax procumbens	(6 ♀ [3 ♀ p]) *G. McPherson 3247*, MO	♀ 6/10 (2/3 p)	♂ 1/1
Poinsettia sp. indet.		–	♂ 1/2
Leucaena leucocephala	*G. McPherson 3237*, MO	♀ 1/1 p	♂ 1/1
Mimosa diplotricha	*G. McPherson 3776*, MO	♀ 1/2 (1/1 p)	–
Psidium guajava		♀ 1/5 p	–
Stenotaphrum secundatum (Walter) Kuntze		♀ 2/2	–
Triumfetta rhomboidea		♀ 2/6 (2/4 p)	–
Stachytarpheta australis Moldenke	*P. Lauri 128*, NOU	–	♂ 1/1
Tribulus cistoides		–	♂ 1/1
–		–	–
sp. indet. 1		–	♂ 1/1
Nephrodesmus ferrugineus Däniker	*J. Munzinger 3011*, NOU	♀ 1/1	–
Homalium betulifolium Däniker		♀ 1/1	–
Dianella sp. indet.		♀ 1/1	–
Agatea rufotomentosa	*J. Munzinger 371*, NOU	♀ 3/3	♂ 1/1
Stachytarpheta australis		♀ 1/1	–
Stachytarpheta cayennensis (Rich.) Vahl		♀ 2/2	–

Abbreviations: BJD, Personal collection of Barry J. Donovan; IRD, Institut de Research pour Développement.

Table 2. Plant families and the number of native and introduced plant genera and species visited by female bees.

Plant families	Number of plant genera	Number of plant species	Number of bee species with females visiting	Number of bee species with females carrying pollen	Number of plant species from which pollen was carried
Native plants					
Aizoaceae	1	1	1	0	0
Apocynaceae	3	4	3	2	2
Araliaceae	4	7	8	6	4
Arecaceae	2	2	5	1+1?	1+1?
Asteraceae	2	2	4	2	2
Boraginaceae	1	1	1	0	0
Celastraceae	1	1	2	0	0
Connaraceae	1	1	2	2	1
Convolvulaceae	1	1	2	0	0
Cunoniaceae	4	9	7	4+1?	4+1?
Dilleniaceae	2	10	9	6+1?	5+2?
Elaeocarpaceae	1	2	1	0	0
Ericaceae	2	3	7	1	1
Escalloniaceae	1	1	1	1	1
Euphorbiaceae	1	2	2	0	0
Fabaceae	5	7	5*	4*	6
Caesalpinoidea	2	4	1	1	4
Mimosoideae	1	1	3	3	1
Papilionoideae	2	2	2	11	1
Flacourtiaceae	1	1	1	1	0
Goodeniaceae	1	5	6	5	4
Joinvilleaceae	1	1	1	1	1
Labiatae	1	1	1	0	0
Liliaceae	2	2	3	0	0
Linaceae	1	1	1	1	1
Loganiaceae	1	1	3	1	1
Malpighiaceae	2	2	3	2	2
Malvaceae	1	1	1	1	1
Melastomataceae	1	2	4	2	2
Myodocarpaceae	1	2	1	1	1
Myoporaceae	1	1	1	0	0
Myrsinaceae	1	1	1	0	0
Myrtaceae	8	21	9	6+1?	11
Onagraceae	1	1	3	2	1
Orchidaceae	1	1	1	0	0
Phellinaceae	1	1	2	0	0
Proteaceae	2	5	5	3	4
Rhamnaceae	1	1	2	0	0
Rhizophoraceae	1	1	1	0	0
Rubiaceae	2	2	4	3	2
Sapindaceae	2	4	4	4	4
Surianaceae	1	1	1	0	0
Tiliaceae	1	1	1	0	0
Violaceae	1	2	5	3	2
Introduced plants					
Amaranthaceae	2	2	2	1	1
Anacardiaceae	1	1	2	2	1
Asteraceae	8	12	7	6	6
Brassicaceae	2	2	2	1	1
Euphorbiaceae	2	3	3	1	2
Fabaceae	8	8	8*	7*	6
Caesalpinioideae	2	2	2	1	1
Mimosoideae	3	3	6	6	3
Papilionoideae	3	3	4	2	2

Table 2. Continued.

Plant families	Number of plant genera	Number of plant species	Number of bee species with females visiting	Number of bee species with females carrying pollen	Number of plant species from which pollen was carried
Lamiaceae	2	2	2	1	1
Lythraceae	1	1	1	1	1
Malvaceae	1	2	2	2	2
Myrtaceae	3	3	3	3	1
Phrymaceae	1	1	1	0	0
Poaceae	1	1	1	0	0
Polygonaceae	2	2	1	0	0
Rutaceae	1	1	1	1	1
Sapindaceae	1	1	4	2+1?	1+1?
Solanaceae	1	3	3	3	3
Tiliaceae	1	1	2	2	1
Verbenaceae	4	7	7	2	2
Zygophyllaceae	1	1	1	1	1
Native or introduced plants (status uncertain)					
Asteraceae	1	1	1	0	0
Convolvulaceae	1	1	2	2	1

? Refers to bee species that carry pollen internally. For example, 4 + 1? means that females of four species were carrying pollen and females of one species were possibly carrying pollen internally.

* Indicates that in these columns, the numbers for the subfamilies of Fabaceae do not match the totals for Fabaceae as a whole. This is because some species of bees visit more than one subfamily.

the 28 recorded by Donovan (1983) and the 21 of Pauly and Munzinger (2003), there is uncertainty as to the number of bee species that might be truly native and the number that might have colonized the country in historic times through agencies of human transport. But if all 43 species are considered, with 3051 species of flowering plants thought to be native to New Caledonia (Morat et al., 2012), the ratio of species of bees to flowering plants is about 1:71. This is extremely low compared to Australia, which lies 1200 km to the west, where the ratio is about 1:7 (Donovan, 1983). However, for New Zealand, which is about 1600 km to the southeast, a recent assessment of 28 native species of bees (Donovan, 2007), and 1612 native species of flowering plants (Allen, 1961; Moore & Edgar, 1976) gives a ratio of 1:57, which suggests that the comparative relationships of native bees and plants of the two island countries may be rather similar.

Apart from *Lithurgus scabrosus* Smith, which is found only on *Ipomoea pes-caprae* (L.) R. Br. (Pauly & Munzinger, 2003), there appear to be no obvious specializations of any species of bees to foraging on particular flowers, and indeed the ablity of the most common species of bees to forage on at least some introduced flowers suggests that their foraging habits are quite plastic. For the uncommon species of bees, the data are too few to allow judgments.

The 116 native species of flowering plants visited by the females of New Caledonian native bees are just 3.8% of the 3051 native species of flowering plants. However, because of height from the ground, the density of foliage, and ruggedness of the landscape, many flowers are difficult to reach with insect collecting equipment, and if access were better there is no doubt that bees would be shown to visit many more flowers. Another major point is that for 20 species of bees there are no records of females associated with flowers. A primary reason for the lack of records is that for several species of bees only one or a few males were collected. Also, if females were collected and especially if very few were collected, there may be no flower records. Only half a dozen species of bees can be considered to be common and perhaps occasionally numerous, of which the primary species are listed in Table 3. A survey of flower visitors at 31 sites over Grande Terre by Kato and Kawakita (2004) found that for 541 individual Apoidea, 89.8% were the introduced honey bee *Apis mellifera*, followed by the Halictidae (6%) and Megachilidae (3%). Colletid bees were not seen. Moreover, honey bees were found in all vegetation types, at every altitude and locality. Kato and Kawakita (2004) concluded that native bees must have been abundant and played an important role in pollination before the immigration of honey bees. They suggest that native bees are now endangered

Table 3. Species of bees with females visiting native and introduced plant families, genera, and species, ranked by the highest number of plant species visited, or for those with equal scores, thereafter as listed in Table 1. Question marks refer to pollen possibly carried internally; P refers to the kleptoparasitic bees of *Lasioglossum*, an undescribed subgenus in which pollen is not collected by females.

Species of bee	Numbers of visited plants			Number of plant species from which pollen was carried
	Families	Genera	Species	
Visitors to native plants				
Austronomia sicheli	22	32	53	29
Homalictus risbeci	18	24	30	15
Homalictus aponi	18	19	27	15
Lasioglossum polygoni	12	16	21	9
Megachile albomarginata	7	8	14	10
Megachile australis	9	10	10	4
Homalictus sp. indet. 4	7	8	9	8
Homalictus sp. indet. 9	4	6	6	2
Euhesma sp. indet. 1	3	3	5	5?
Homalictus sp. indet. 8	4	4	5	3
Lasioglossum sp. indet. 4	5	5	5	0
Megachile aurantiaca	4	4	4	0
Homalictus cocos	2	2	2	0
Homalictus sp. indet. 6	2	2	2	1
Megachile laticeps	2	2	2	0
Leioproctus pacificus	1	1	1	0
Palaeorhiza flavomellea	1	1	1	1?
Lasioglossum sp. indet. 7	1	1	1	0
Lasioglossum sp. indet. 9	1	1	1	P
Lithurgus scabrosus	1	1	1	0
Megachile umbripenne	1	1	1	1
Visitors to introduced plants				
Homalictus aponi	9	19	24	14
Austronomia sicheli	10	13	14	8
Megachile australis	7	10	11	5
Megachile albomarginata	6	10	10	8
Homalictus risbeci	6	9	9	6
Lasioglossum polygoni	6	7	7	5
Homalictus cocos	3	3	3	1
Homalictus sp. indet. 8	2	2	2	1
Ceratina dentipes	1	1	2	0
Euryglossina sp. indet. 1	1	1	1	1?
Austronomia sp. indet. 3	1	1	1	0
Megachile umbrippenne	1	1	1	1
Visitors to native or introduced plants (status uncertain)				
Homalictus sp. indet. 4	4	1	1	0
Austronomia sicheli	1	1	1	1
Lithurgus scabrosus	1	1	1	1

because of competitive pressure from honey bees, and that original plant-pollinator interactions have been altered.

Although direct evidence of competitive interactions between native bees and honey bees has not yet been documented, our findings that most species of native bees are very uncommon strongly support the opinions of Kato and Kawakita (2004). Because honey bees forage for nectar and pollen whenever weather allows them to, and they are extremely polylectic, native bees in tropical New Caledonia are faced with continuous competitive foraging pressure from this introduced bee. Unless honey bee numbers are reduced, perhaps by the future occurrence of the mite *Varroa destructor* Anderson & Trueman, the survival of most of the native species of bees in New Caledonia may be uncertain, which would forever obscure the original relationships between them and the native flora.

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THE ORTHOSIINAE REVISITED (APOCYNACEAE, ASCLEPIADOIDEAE, ASCLEPIADEAE)[1]

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ABSTRACT

The subtribe Orthosiinae (Apocynaceae, Asclepiadoideae, Asclepiadeae) is monophyletic and comprises four genera. *Monsanima* Liede & Meve is herein validly established, comprising one species, *M. morrenioides* (Goyder) Liede & Meve. This new genus is sister to a clade consisting of *Jobinia* E. Fourn., *Orthosia* Decne., and *Scyphostelma* Baill. A taxonomic key to these four genera is provided. For *Jobinia*, one species, *J. peruviana* Liede & Meve, is newly described, and 13 species previously treated principally under *Cynanchum* L. are transferred, so that the genus now comprises 25 species. *Jobinia fontellana* Liede & Meve is proposed as a new name, replacing *O. hatschbachii* Fontella & Goes. The following new combinations are made in *Jobinia*: *J. canoi* (Morillo) Liede & Meve, *J. formosa* (N. E. Br.) Liede & Meve, *J. latipes* (Decne.) Liede & Meve, *J. mazzuchii* (Speg.) Liede & Meve, *J. samuelssonii* (Malme) Liede & Meve, *J. schizocorona* (Liede & Meve) Liede & Meve, *J. streptantha* (Malme) Liede & Meve, *J. tarmensis* (Schltr.) Liede & Meve, *J. tiarata* (Malme) Liede & Meve, *J. trifurcata* (Griseb.) Liede & Meve, and *J. umbellata* (Rusby) Liede & Meve. In *Orthosia*, the new combination *O. angustifolia* (Turcz.) Liede & Meve is made. *Orthosia thymifolia* Schltr. is excluded from the genus and the new combination *Ditassa thymifolia* (Schltr.) Liede & Meve (Metastelmatinae) is proposed. The genus *Scyphostelma* is reinstated, and 26 species, most previously in *Cynanchum*, are transferred: *S. beckii* (Morillo) Liede & Meve, *S. bifida* (Liede & Meve) Liede & Meve, *S. brachyphylla* (K. Schum.) Liede & Meve, *S. carmenaemiliae* (Morillo) Liede & Meve, *S. chimboracensis* (Morillo) Liede & Meve, *S. confusa* (R. W. Holm) Liede & Meve, *S. ecuadorensis* (Schltr.) Liede & Meve, *S. filisepala* (Standl.) Liede & Meve, *S. harlingii* (Morillo) Liede & Meve, *S. intricata* (K. Schum.) Liede & Meve, *S. isidrensis* (Morillo) Liede & Meve, *S. lechleri* (Morillo) Liede & Meve, *S. longecalicina* (Morillo) Liede & Meve, *S. luteynii* (Morillo) Liede & Meve, *S. microphylla* (Kunth) Liede & Meve, *S. nubicola* (Morillo) Liede & Meve, *S. pichinchensis* (K. Schum.) Liede & Meve, *S. ruizteranii* (Morillo) Liede & Meve, *S. serpyllifolia* (Kunth) Liede & Meve, *S. siderocalyx* (Morillo) Liede & Meve, *S. sodiroi* (K. Schum.) Liede & Meve, *S. tenella* (L. f.) Liede & Meve, *S. trianae* (Schltr.) Liede & Meve, *S. veleziae* (Morillo) Liede & Meve, *S. velutina* (Morillo) Liede & Meve, and *S. wurdackii* (Morillo) Liede & Meve. Ten names are lectotypified: *C. ecuadorense* Schltr., *J. formosa*, *J. tarmensis*, *J. tiarata*, *J. trifurcata*, *J. umbellata*, *S. brachyphylla*, *S. ecuadorensis*, *S. intricata*, and *S. pichinchensis*. Three names are neotypified: *J. chlorantha* (K. Schum.) Malme, *S. sodiroi*, and *S. trianae*.

Key words: Apocynaceae, Asclepiadoideae, Central America, *Cynanchum*, *Jobinia*, *Monsanima*, *Orthosia*, Orthosiinae, *Scyphostelma*, South America.

Orthosia Decne. was described by Decaisne (1844), based on *O. congesta* (Vell.) Decne., a Brazilian species, and Decaisne also attributed five more species to *Orthosia*: *O. umbrosa* Decne., *O. kunthii* Decne., *O. serpyllifolia* (Kunth) Decne., *O. arenosa* Decne., and *O. suberosa* Decne. By 1932, Fournier, Grisebach, Malme, and Schlechter added some 20 additional names to the genus. However, *Orthosia* was associated with those genera merged under the extended concept of *Cynanchum* L. by Woodson (1941). Only Fontella Pereira and Valente (1969) would thereafter publish a species under this generic name as *O. loandensis* Fontella & C. Valente, but they did so without comment on the generic circumscription of the taxa. Liede (1997), based on morphological studies, rejected the enlarged genus sensu Woodson (1941) for *Cynanchum* and suggested the reinstatement of *Orthosia* to include *Amphistelma* Griseb. She (Liede, 1997) listed 61 names considered to belong to *Orthosia*, of which 22 were so far known

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under *Orthosia*, with 10 names under *Amphistelma*, 24 in *Cynanchum*, four in *Metastelma* R. Br., and one within *Tassadia* Decne. However, Liede (1997) refrained from large-scale nomenclatural changes, suspecting a high degree of synonymy in these names, of which many were applicable to incompletely known taxa. The independence of *Orthosia* from *Cynanchum* was demonstrated hence by molecular studies (Liede & Täuber, 2002).

Recent molecular studies (Rapini et al., 2003, 2006; Liede-Schumann et al., 2005) have shown that more than three quarters of the roughly 1000 American species of the Asclepiadoideae (Meve, 2002) belong to a single large radiation, termed the MOOG clade (Liede-Schumann et al., 2005: fig. 1). The MOOG clade comprises the four subtribes Metastelmatinae Endl. ex Meisn., Orthosiinae Liede & Rapini, Oxypetalinae E. Fourn., and Gonolobinae G. Don ex Liede, each with several genera, and three genera not attributable at present to any of these subtribes (*Pentacyphus* Schltr., *Diplolepis* R. Br., and *Tassadia*).

Although Gonolobinae and Oxypetalinae morphologically constitute easily recognizable units of long taxonomic recognition (e.g., Schumann, 1895), the separation of Orthosiinae from Metastelmatinae was unsuspected. However, Woodson (1941) actually did include members from both subtribes into his enlarged *Cynanchum*. This background, together with the insignificant and hard-to-distinguish flowers for many taxa of the Orthosiinae and Metastelmatinae, has for a long time hampered our taxonomic understanding of these two subtribes and of American Asclepiadoideae as a whole.

From the analysis of Liede-Schumann et al. (2005) and that of Rapini et al. (2007), it became apparent that Orthosiinae, aside from *Orthosia* and *Jobinia* E. Fourn., encompasses many species of Woodson's (1941) enlarged *Cynanchum* that do not immediately associate with *Orthosia* morphologically. Following molecular evidence for *Orthosia* and the Orthosiinae, new species were again published under this name by Stevens (2005), and the process of sorting the old American names in *Cynanchum* among molecularly supported, monophyletic genera was initiated by Liede-Schumann and Meve (2008). The present publication is intended to elucidate the structure of the subtribe Orthosiinae by adding both more taxa and more molecular markers than in Liede-Schumann et al. (2005). With this increased support, such a rigorous generic delimitation can serve as taxonomic framework for the overdue revision of the Orthosiinae.

Materials and Methods

Taxon and outgroup selection

As a starting point, the matrix of Liede-Schumann et al. (2005) was used. Outgroup samples for which *rps16* sequence data were missing were removed from the analyses. Thus, two samples of *Pentacyphus*, six of *Diplolepis*, three of *Tassadia*, seven Gonolobinae, 31 Metastelmatinae, and 37 Oxypetalinae, adding up to 86 taxa, constituted the outgroup. Following the results of Liede-Schumann et al. (2005) and Rapini et al. (2007), two samples of *Pentacyphus* were selected as the most distant outgroup. For some outgroup taxa in Metastelmatinae, different accessions were used to amplify different primer regions (Table 1), especially in cases where sequences from previous studies were available for some primers but better material had been collected in the meantime. Sequence information for these taxa was then combined to represent the species.

As ingroup, 61 samples presumably belonging to Orthosiinae were added (one accession of an undescribed genus, 12 for *Jobinia*, 33 for *Orthosia*, 15 for *Scyphostelma* Baill.). For the ingroup, we accepted only those samples with no more than one partial sequence missing, and all sequence information refers to the level of a particular accession (see Table 1).

DNA extraction, polymerase chain reaction (PCR) amplification, and sequencing

DNA was extracted from silica-dried leaves (vouchers held at UBT) or from leaf fragments taken from herbarium specimens held at B, CORD, FR, HUEFS, MJG, MO, MSUN, NY, S, and SPF. Total DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. Several DNA samples from previous studies were also used (Liede, 2001; Liede & Meve, 2002; Liede & Täuber, 2002; Liede-Schumann et al., 2005; Silva et al., 2012). PCR primers and protocols for the plastid *trnT–trnL* and *trnL–trnF* spacers and the *trnL* intron correspond to those in Taberlet et al. (1991). The *trnL* intron and *trnL–trnF* intergenic spacer were amplified either as a single fragment using primers "c" and "f," or as two separate fragments using primer pairs "c" and "d" and "e" and "f," respectively. For purposes of alignment, the two amplified segments were kept separate, because most of the older samples had also been amplified separately. The *rps16* intron was amplified as in Liede-Schumann et al. (2005), using

the primer pair rps16-1F and rps16-2R; however, amplification failed for seven ingroup samples.

An additional region, the *trnD–trnT* spacer as described by Shaw et al. (2005), was amplified for the ingroup taxa, because it provided a higher resolution than previously used markers. PCR primers followed Shaw et al. (2005), but with 94°C (3 min.) initial denaturation and 30 cycles of 93°C (1 min.), 55°C (2 min.), 72°C (3 min.), with a final phase of 72°C (5 min.). For sequencing, the primers trnE (5′-AGG ACA TCT CTC TTT CAA GGA G-3′), trnY (5′-CCG AGC TGG ATT TGA ACC A-3′), and the internal primer trnY-i (5′-CGG ATA ACT TGT TGA TTC GTC ATT C-3′), designed for American Asclepiadeae, were used.

For the ingroup, six taxa could not be amplified for the *trnD–trnT* spacer. The high variability of the *trnD–trnT* spacer, on the other hand, led to aligning problems with the more distant outgroups. Therefore, it was amplified for all except one of the Metastelmatinae, but not across the entire outgroup. The remaining outgroup taxa were therefore coded "?" for the 1592 positions of the *trnD–trnT* spacer. Furthermore, as the protocol for the amplification of the *trnD–trnT* spacer was developed during this study, the length of the 5′ end was highly variable and was found to lack approximately the first 250 bp in the older sequences. Nevertheless, all available sequence information was included in this study, following Hughes and Vogler (2004), so that as many characters as possible could be included in an analysis.

ALIGNMENT AND PHYLOGENY RECONSTRUCTIONS

For most regions, alignment was fairly straightforward, and the new sequences could be added to the existing datasets using MESQUITE (Maddison & Maddison, 2010) and alignment results were adjusted manually. For the *trnD–trnT* spacer, alignments with ClustalW2 (Chenna et al., 2003) and Muscle (Edgar, 2004), available at the European Molecular Biology Laboratory (EMBL) (<http://www.ebi.ac.uk/Tools/sequence.html>) were performed with various settings, leading to rather homogeneous blocks both in Metastelmatinae and Orthosiinae, which were then manually adjusted. The matrix has been submitted to TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S12128>). The best-fitting model for the five partial nucleotide datasets was selected with jModelTest version 0.1.1 (Posada, 2008); for model selection, taxa missing the particular partial sequence were removed. A set of 24 models was tested for Bayesian inference analysis (BI), and the full set of 88 models was tested for maximum likelihood analysis (ML).

BI of the combined dataset was performed with MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), using the best models retrieved with jModeltest (see Table 2). Four runs with four Markov chains (one cold, three heated) were run for 10,000,000 generations, saving one tree every 1000 generations. Analyses were diagnosed for convergence using AWTY (Are We There Yet?) (Wilgenbusch et al., 2004). The AWTY plot of chain variability suggested a burn-in of 6000 trees before log-likelihoods were stabilized. The remaining 4000 trees from all runs (16,000 trees in total) were summarized as majority rule consensus with the percentages on the branches indicating the Bayesian posterior probabilities (PP). PP values $> 95\%$ were considered to indicate very strong support, 85%–94% strong support, 75%–84% moderate support, and $< 75\%$ poor support. Since the best model under the Akaike information criterion corrected for small datasets (AICc; Burnham & Anderson, 2003) was in some cases different from the model selected under the uncorrected Akaike information criterion or the Bayesian information criterion (BIC, Schwarz, 1978), the analysis was repeated with the other model to trace incongruencies.

ML of the nucleotide dataset was performed with GARLI 2.0 (Zwickl, 2006), which allows the use of different models for the different partitions of the dataset. The best models retrieved with jModeltest out of the 88 models available were implemented and five search replicates (searchreps = 5) were conducted. Branch support was estimated with 100 bootstrap replicates, with two search replicates for each run.

Maximum parsimony analysis (MP) was performed using Fitch parsimony as implemented in PAUP* version 4.0b10 (Swofford, 2002) using heuristic searches, with 1000 addition sequence replicates, random stepwise addition, MULTREES off, and tree-bisection-reconnection (TBR) branch swapping. The resulting trees were then used as starting trees for a second round of search with MULTREES on. The sets of equally parsimonious trees recovered from the analyses were summarized by strict consensus. To estimate branch support, a bootstrap analysis was run with 10,000 replicates, each with 10 addition sequence replicates, TBR branch swapping, MULTREES on, and MAXTREES set to 10. Bootstrap values (MP and ML) above 90% were considered to indicate very strong support, 80%–89% strong support, 70%–79% moderate support, and $< 70\%$ poor support.

Results

Sequence characteristics and models selected are summarized in Table 2. BI analysis did not converge at an average standard deviation < 0.01, which indicates very good convergence, but after six million generations an average standard deviation < 0.03 was reached, which is regarded as adequate for most analyses (Ronquist et al., 2011). In the ML analysis, the best tree found by GARLI reached a score of −16771.50939. All five of the best trees retrieved display an identical topology except for the position of *Philibertia discolor* (Schltr.) Goyder in Oxypetalinae, which is placed outside *Philibertia* Kunth in one of these five trees. MP analysis yielded more than 38,300 trees (limit of computer capacity; length (L) = 864 steps, consistency index (CI) = 0.61, retention index (RI) = 0.91, rescaled consistency index (RC) = 0.56).

BI, ML, and MP analyses yielded highly congruent trees (trees summarized in Fig. 1). Bootstrap support values (BS) for ML and MP were in general lower than PP values and, for most clades, very similar to each other. The monophyly of the Orthosiinae was well supported by BI and ML analyses, but was only moderately supported by the parsimony bootstrap (70% BS, not shown). The trichotomy of Orthosiinae, *Diplolepis*, and the group composed of Metastelmatinae, *Tassadia*, Gonolobinae, and Oxypetalinae was not resolved in any analysis. *Tassadia*, Gonolobinae, and Oxypetalinae also formed a trichotomy in all analyses and were sister to Metastelmatinae. All major taxonomic groups were well supported in Bayesian and likelihood analysis, but some were only moderately supported by the parsimony bootstrap.

Clade structure in the Orthosiinae was likewise clear cut and well supported in our analyses. The new genus established herein was sister to all other Orthosiinae, a result obtained in Liede-Schumann et al. (2005) as well. *Scyphostelma* was sister to a well-supported clade composed of *Jobinia* and *Orthosia*, all well supported.

In *Jobinia*, four subclades were retrieved (Fig. 1): *J. formosa* (N. E. Br.) Liede & Meve (transferred herein) took an isolated unresolved position in this clade; one subclade comprises specimens from Ecuador and Peru (including the new *J. peruviana* Liede & Meve, and the new combinations *J. streptantha* (Malme) Liede & Meve and *J. tarmensis* (Schltr.) Liede & Meve); one subclade comprises southern Andean species (*J. umbellata* (Rusby) Liede & Meve and *J. trifurcata* (Griseb.) Liede & Meve, these consolidated as transfers to *Jobinia* herein); and one subclade comprises species from northern Argentina and Brazil (including the new combination *J. latipes* (Decne.) Liede & Meve, as well as *J. chlorantha* (K. Schum.) Malme, *J. hatschbachii* Fontella & E. A. Schwarz, and *J. lindbergii* F. Fourn.). All subclades were very well supported by all analyses. However, a sister group relationship between the "Brazilian" and the "southern Andean" subclades is only suggested by ML and remains without support. In the other analyses, the three *Jobinia* subclades remain unresolved.

While species-level resolution inside *Orthosia* and *Scyphostelma* was not the aim of the present study, and indeed was not obtained in all cases, it is noteworthy that quite often morphologically similar accessions identified to a particular species were not retrieved as a monophyletic group. This was exemplified by the 10 samples of *O. scoparia* (Nutt.) Liede & Meve, where one collection from Bolivia (*Wood 15776*) was retrieved consistently as sister to all other *Orthosia* species (Fig. 1A). Likewise, the two mainland South American samples of *O. scoparia* (*Wasum 7930* from Brazil and *van der Werff 7441* from Venezuela) were not members of the very well-supported *O. scoparia* clade, which included accessions only of Caribbean provenance.

The Argentinean and Bolivian samples (*Orthosia pearcei* (Rusby) Liede & Meve, *O. virgata* (Poir.) E. Fourn., and *Orthosia* sp. indet. a [*Liede et al. 3640*]) were strongly supported as monophyletic, even though *O. virgata* significantly diverged with a unique 10-bp insert in the *rps16* intron. This clade was sister to a clade comprising specimens of both South American and Central American origin, in which the South American samples tended to occupy positions closer to the base. In this clade, *O. kunthii*, *O. angustifolia* (Turcz.) Liede & Meve (new combination herein), and *O. pubescens* (Greenm.) Liede & Meve are represented by two accessions each, which are retrieved as monophyletic subclades. In contrast, the three accessions of *O. bonplandiana* (Schult.) Liede & Meve from Bolivia (*Wood et al. 13292*), Venezuela (*Liede & Meve 3311*), and Mexico (*Conrad 9306*) appeared in different positions of the South American–Central American clade. The Mexican accession grouped weakly with the two accessions of the Mexican *O. pubescens*, and the Bolivian accession with the two Ecuadorian accessions of *O. ellemannii* (Morillo) Liede & Meve, while the third accession took an unresolved position in the South American–Central American *Orthosia* clade. Likewise, of the three samples of *O. ellemannii* from Ecuador, only two nested in the same clade, together with an *O. bonplandiana* sample from Bolivia, while the third accession took an unresolved position in the

Table 1. Exemplar species of the Orthosiinae included in this study, with herbarium vouchers and European Molecular Biology Laboratory (EMBL) accession numbers in support of the molecular phylogeny (cf. Fig. 1). Partial sequences marked "–" were not obtained.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Outgroup							
Pentacyphus andinus (Ball) Liede	*Liede & Meve 3451* (UBT)	Peru	AJ492149	AJ492150	AJ492151	AJ699335	–
Pentacyphus lehmannii (Schltr.) Liede	*Liede 3333* (cult. Bayreuth)	Ecuador	AJ290890	AJ290889	AJ290888	AJ704928	–
Diplolepis boerhaviifolia (Hook. & Arn.) Liede & Rapini	*Liede & Conrad 3062* (MSUN, ULM)	Chile	AJ428606	AJ428607	AJ428608	AJ699331	–
Diplolepis descolei (T. Mey.) Liede & Rapini	*Naumann 1347* (MB)	Argentina	AJ699301	AJ699304	AJ699302	AJ699303	–
Diplolepis geminiflora (Decne.) Liede & Rapini	*Heyne 103* (MSUN)	Chile	AJ410181	AJ410182	AJ410183	AJ699332	–
Diplolepis hieronymi (Lorentz) Liede & Rapini	*Liede & Conrad 3052* (MSUN, ULM)	Argentina	AJ410211	AJ410212	AJ410213	AJ699333	–
Diplolepis menziesii Schult.	*Liede & Conrad 3060* (K, MSUN, ULM)	Chile	AJ699274	AJ699273	AJ699275	AJ699276	–
Diplolepis nummulariifolia (Hook. & Arn.) Liede & Rapini	*Liede & Conrad 3050* (MO, MSUN, ULM)	Argentina	AJ290853	AJ290852	AJ290851	AJ699334	–
Tassadia berteroana (Spreng.) W. D. Stevens	*Nee 36277* (NY)	Bolivia	AJ428789	AJ428790	AJ428791	AJ699336	–
Tassadia guianensis Decne.	*Wolff 528* (UBT)	Ecuador	AJ699278	AJ699280	AJ699279	AJ699277	–
Tassadia obovata Decne.	*Matezki 332* (UBT)	Ecuador	AJ699282	AJ699281	AJ699283	AJ699284	–
Gonolobinae							
Gonolobus barbatus Kunth	*Conrad 9325* (UBT)	Mexico	AJ704262	AJ704261	AJ704263	AJ704264	–
Gonolobus parviflorus Decne.	*Rapini 609* (SPF)	Brazil	AJ704528	AY163689	AY163689	AJ704529	
Macroscepis hirsuta (Vahl) Schltr.	*Heyne s.n.* (UBT)	Guatemala	AJ704266	AJ704268	AJ704267	AJ704265	–
Matelea cyclophylla (Standl.) Woodson	*Barad s.n.* (UBT)	Mexico	AJ704271	AJ704269	AJ704272	AJ704273	–
Matelea gonocarpa (Walter) Shinners	*ex Wyatt s.n.* (GA)	U.S.A.	AJ704275	AJ704277	AJ704276	AJ704274	–
Matelea pedalis (E. Fourn.) Fontella & E. A. Schwarz	*Rapini 714* (SPF)	Brazil	AJ704531	AY163699	AY163699	AJ704530	
Schubertia grandiflora Mart. & Zucc.	*Liede & Conrad 3033* (MSUN, UBT, ULM)	Argentina	AJ428825	AJ428826	AJ428827	AJ699364	–
Metastelmatinae							
Barjonia chlorifolia Decne.	*Rapini 485* (SPF)	Brazil	–	AY163667	AY163667	AJ704463	–
	Rapini 1395 (SPF)	Brazil	JN701896	–	–	–	JN574510
Blepharodon glaucescens (Decne.) Fontella	*Ollerton 187* (UBT)	Guyana	AJ699290	AJ699289	AJ699291	AJ699292	HE611884
Blepharodon grandiflorum Benth.	*Liede & Meve 3318* (UBT)	Venezuela	AJ290836	AJ290837	AJ290838	AJ699337	HE611885
Blepharodon lineare (Decne.) Decne.	*Forzza 2027* (SPF)	Argentina	AJ704465	AY163668	AY163668	AJ704466	–
Blepharodon mucronatum (Schltdl.) Decne.	*Liede 3243* (UBT)	Belize	AJ290841	AJ290840	AJ290839	AJ699338	HE611886
Blepharodon pictum (Vahl) W. D. Stevens	*Rapini 938* (SPF)	Brazil	AJ704468	AY163669	AY163669	AJ704467	–
	Queiroz 9196 (HUEFS)		–	–	–	–	JN574516
Ditassa anderssonii Morillo	*Matezki SM 141* (UBT)	Ecuador	HE611702	HE611761	HE611800	HE611839	HE611887
Ditassa banksii R. Br. ex Schult.	*Konno 754* (SPF)	Brazil	AJ704474	AY163674	AY163674	AJ704473	JN574518
Ditassa burchellii Hook. & Arn.	*Krapovickas 41170* (NY)	Argentina	AJ699294	AJ699296	AJ699295	AJ699293	JN574519

Table 1. Continued.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Ditassa endoleuca Schltr.	*Liede & Meve 3564* (UBT)	Ecuador	HE611703	HE611762	HE611801	HE611840	HE611888
Ditassa hispida (Vell.) Fontella	*Konno 779* (SPF)	Brazil	AJ704479	AJ704478	AJ704480	AJ704477	–
	Rapini 1431 (HUEFS)	Brazil	–	–	–	–	JN574526
Ditassa mucronata Mart.	*Arbo et al. 3885* (NY)	Brazil	AJ704270	AJ704259	AJ704278	AJ704279	–
	Rapini 1077 (HUEFS)	Brazil	–	–	–	–	JN574527
Ditassa obcordata Mart.	*Cervi 4073* (NY)	Brazil	AJ428750	AJ428751	AJ428752	AJ699340	–
	Rapini 1050 (HUEFS)	Brazil	–	–	–	–	JN574528
Ditassa retusa Mart.	*Coradin et al. 6075* (NY)	Brazil	AJ704281	AJ704283	AJ704282	AJ704280	–
	Rapini 1362 (HUEFS)	Brazil	–	–	–	–	JN574530
Ditassa tomentosa (Decne.) Fontella	*Konno 780* (SPF)	Brazil	AJ704485	AJ704484	AJ704486	AJ704483	–
	Rapini 616 (HUEFS)	Brazil	–	–	–	–	JN574531
Ditassa thymifolia (Schltr.) Liede & Meve	*Weigend et al. 8606* (B, USM)	Peru: Cajamarca	HE611735	HE611788	HE611827	HE611870	HE611929
Hemipogon acerosus Decne.	*Wood & Goyder 15689* (K)	Bolivia	AJ704289	AJ704291	AJ704290	AJ704288	–
	Rapini 1875 (HUEFS)	Brazil	–	–	–	–	JN574533
Hemipogon andinum Rusby	*Wood & Wasshausen 16626* (K)	Bolivia	AJ704293	AJ704292	AJ704294	AJ704295	HE611889
Hemipogon sprucei E. Fourn.	*Wood & Goyder 15719* (K)	Bolivia	AJ704297	AJ704299	AJ704298	AJ704296	–
	Soares e Silva 106 (HUEFS)	Brazil	–	–	–	–	JN574537
Metastelma linearifolium A. Rich.	*Urquiola et al. 561* (FR)	Cuba	AJ428807	AJ428808	AJ428809	AJ699341	JN574541
Metastelma parviflorum (Sw.) R. Br. ex Schult.	*Liede & Meve 3328* (UBT)	Venezuela	AJ428777	AJ428778	AJ428779	AJ699342	JN574543
Metastelma schaffneri A. Gray	*Liede & Conrad 2962* (UBT)	Mexico	AJ410214	AJ410215	AJ410216	AJ699343	JN574544
Minaria acerosa (Mart.) T. U. P. Konno & Rapini	*Ribas & Santos 889* (NY)	Brazil	AJ699286	AJ699288	AJ699287	AJ699285	–
	Ribeiro 183 (HUEFS)	Brazil	–	–	–	–	JN574545
Minaria decussata (Mart.) T. U. P. Konno & Rapini	*Arbo et al. 4039* (NY)	Brazil	AJ704218	AJ704220	AJ704219	AJ704217	–
	Rapini 909 (HUEFS)	Brazil	–	–	–	–	JN574546
Minaria grazielae (Fontella & Marquete) T. U. P. Konno & Rapini	*Omlor 147* (MJG)	Brazil	AJ410202	AJ410203	AJ410204	AJ699339	HE611890
Minaria magisteriana (Rapini) T. U. P. Konno & Rapini	*Rapini 597* (SPF)	Brazil	AJ704481	AY163681	AY163681	AJ704482	–
	Ribeiro 200 (HUEFS)	Brazil	–	–	–	–	JN574549
Nautonia nummularia Decne.	*Liede & Conrad 3031* (ULM)	Argentina	AJ410226	AJ 410227	AJ410228	AJ699344	HE611891
Nephradenia acerosa Decne.	*Philcox 3303* (K)	Brazil	AJ704497	AY163704	AY163705	AJ704496	–
	Soares e Silva 118 (HUEFS)		–	–	–	–	JN574551
Nephradenia asparagoides (Decne.) E. Fourn.	*Irwin 13012* (K)	Brazil	AJ704498	AY163706	AY163707	AJ704499	–
	Soares e Silva 01 (HUEFS)		–	–	–	–	JN574552

Table 1. Continued.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Peplonia asteria (Vell.) Fontella & E. A. Schwarz	*Fontella sub Konno 773* (SPF)	Brazil	AJ704301	AJ704300	AJ704302	AJ704303	HE611892
Peplonia organensis (E. Fourn.) Fontella & Rapini	*Konno 854* (SPF)	Brazil	AJ704487	AY163688	AY163688	AJ704488	JN574555
Petalostelma sarcostemma (Lillo) Liede & Meve	*Liede & Conrad 3090* (MSUN, ULM)	Argentina	AJ428786	AJ428787	AJ428788	AJ699345	JN574557
Oxypetalinae							
Araujia angustifolia Steud.	*Liede & Conrad 3012* (UBT)	Argentina	AJ699290	AJ699289	AJ699291	AJ704333	–
Araujia plumosa Schltr.	*Liede & Conrad 3070* (MSUN, ULM)	Argentina	AJ704335	AJ704337	AJ704336	AJ704334	–
Araujia sericifera Brot.	*Liede & Conrad 3007* (ULM)	Argentina	AJ428792	AJ428793	AJ428794	AJ699352	–
Funastrum angustifolium (Pers.) Liede & Meve	*Liede & Conrad 3401* (UBT)	U.S.A.	AJ428759	AJ428760	AJ428761	AJ699353	–
Funastrum arenarium (Decne. ex Benth.) Liede	*Liede & Conrad 2952* (GA, ULM)	Mexico	AJ290859	AJ290858	AJ290857	AJ699354	–
Funastrum clausum (Jacq.) Schult.	*Liede & Conrad 2599* (MO, MSUN)	Mexico	AJ290860	AJ290861	AJ290862	AJ699355	–
Funastrum odoratum (Hemsl.) Schltr.	*Liede & Conrad 2560* (MO, MSUN)	Mexico	AJ290871	AJ290870	AJ290869	AJ699356	–
Morrenia odorata (Hook. & Arn.) Lindl.	*Liede & Conrad 3009* (MO, MSUN, ULM)	Argentina	AJ704343	AJ704345	AJ704344	AJ704342	–
Oxypetalum balansae Malme	*Liede & Conrad 3015* (ULM)	Argentina	AJ704347	AJ704346	AJ704348	AJ704349	–
Oxypetalum banksii Schult.	*Rapini 911* (SPF)	Brazil	AJ704503	AY163710	AY163710	AJ704502	
Oxypetalum brachystemma Malme	*Liede & Conrad 3069* (MSUN, ULM)	Argentina	AJ704351	AJ704353	AJ704352	AJ704350	–
Oxypetalum capitatum Mart.	*Mello-Silva 1923* (SPF)	Argentina	AJ704504	AY163711	AY163711	AJ704505	–
Oxypetalum coccineum Griseb.	*Galetto 562* (CORD)	Argentina	AJ704328	AJ704329	AJ704326	AJ704327	–
Oxypetalum coeruleum (D. Don ex Sweet) Decne.	*Liede & Conrad s.n.* (ULM)	Argentina	AJ704355	AJ704354	AJ704356	AJ704357	–
Oxypetalum dactylostelma Goyder	*Wood 15195* (K, UBT)	Bolivia	AJ704339	AJ704338	AJ704340	AJ704341	–
Oxypetalum lanatum Decne. ex E. Fourn.	*Rapini 929* (SPF)	Brazil	AJ704509	AJ704507	AJ704508	AJ704506	–
Oxypetalum minarum E. Fourn.	*Rapini 908* (SPF)	Brazil	AJ704510	AY163713	AY163713	AJ704511	–
Oxypetalum pannosum Decne.	*Rapini 935* (SPF)	Brazil	AJ704515	AJ704513	AJ704514	AJ704512	–
Oxypetalum pentasetum (Rusby) Goyder & Rapini	*Liede & Conrad 3128* (ULM)	Bolivia	AJ704253	AJ704252	AJ704254	AJ704255	–
Oxypetalum solanoides Hook. & Arn.	*Liede & Conrad 3004* (MO, MSUN, ULM)	Argentina	AJ704359	AJ704361	AJ704360	AJ704358	–
Oxypetalum sublanatum Malme	*Rapini 937* (SPF)	Brazil	AJ704516	AY163715	AY163715	AJ704517	–
Oxypetalum sylvestre (Hook. & Arn.) Goyder & Rapini	*Liede & Conrad 3024* (K, MO, MSUN, ULM)	Argentina	AJ410244	AJ410245	AJ410246	AJ699363	–
Oxypetalum warmingii (E. Fourn.) Fontella & Marquete	*Rapini 906* (SPF)	Brazil	AJ704521	AJ704519	AJ704520	AJ704518	–
Oxypetalum wightianum Hook. & Arn.	*Rapini 705* (SPF)	Brazil	AJ704522	AJ704524	AJ704523	AJ704525	–
Philibertia boliviana (Baill.) Goyder	*Wood et al. 15286* (K)	Bolivia	AJ704231	AJ704233	AJ704232	AJ704230	–
Philibertia candolleana (Hook. & Arn.) Goyder	*Liede & Conrad 3055* (ULM)	Argentina	AJ410175	AJ410176	AJ410177	AJ699357	–

Table 1. Continued.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Philibertia discolor (Schltr.) Goyder	*Mello-Silva 1887* (SPF)	Argentina	AJ704527	AY163700	AY163700	AJ704526	–
Philibertia fontellae Goyder	*Wood & Goyder 15543* (K, UBT)	Bolivia	AJ492152	AJ492153	AJ492154	AJ699358	–
Philibertia gilliesii Hook. & Arn.	*Liede & Conrad 3054* (MO, MSUN, ULM)	Argentina	AJ290896	AJ290895	AJ290894	AJ699359	–
Philibertia globiflora Goyder	*Wood 15803* (K, UBT)	Bolivia	AJ704235	AJ704234	AJ704236	AJ704238	–
Philibertia latiflora (Griseb.) Goyder	*Liede & Conrad 3091* (MSUN, ULM)	Argentina	AJ704240	AJ704242	AJ704241	AJ704239	–
Philibertia lysimachioides (Wedd.) T. Mey.	*Liede & Conrad 3139* (MSUN, ULM)	Bolivia	AJ290902	AJ290901	AJ290900	AJ699360	–
Philibertia multiflora (T. Mey.) Goyder	*Wood & Serrano 14466* (K, UBT)	Bolivia	AJ704244	AJ704243	AJ704245	AJ704246	–
*Philibertia parviflor*a (Malme) Goyder	*Liede & Conrad 3113* (UBT)	Argentina	AJ410223	AJ410224	AJ410225	AJ699361	–
Philibertia peduncularis (Benth.) Goyder	*Wood & Goyder 15444* (K, UBT)	Bolivia	AJ704249	AJ704251	AJ704250	AJ704247	–
Philibertia picta Schltr.	*Liede & Conrad 3104* (K, MO, MSUN, ULM)	Argentina	AJ290903	AJ290904	AJ290905	AJ699362	–
Tweedia brunonis Hook. & Arn.	*Liede & Conrad 3058* (UBT)	Argentina	AJ704257	AJ704260	AJ704258	AJ704256	–
Ingroup							
Jobinia chlorantha (K. Schum.) Malme	*Wolff 110* (UBT)	Ecuador: Zamora-Chinchipe	HE611704	HE611751	HE611751	HE611842	HE611893
Jobinia formosa (N. E. Br.) Liede & Meve	*Liede & Conrad 3061* (MSUN)	Chile: Coquimbo	AJ428639	AJ428640	AJ428641	AJ699346	HE611900
Jobinia hatschbachii Fontella & E. A. Schwarz	*Konno 856* (SP)	Brazil: São Paulo	HE611705	HE611763	HE611802	HE611842	HE611894
Jobinia latipes (Decne.) Liede & Meve	*Tressens et al. 6647* (CTES, UBT)	Argentina: Misiones	HE611706	HE611764	HE611803	HE611843	HE611895
Jobinia lindbergii E. Fourn.	*Farinaccio 194* (SPF)	Brazil	AJ704491	AY163694	AY163694	AJ704490	–
Jobinia peruviana Liede & Meve	*Hutchinson & Wright 5439* (S)	Peru: Cajamarca	HE611707	HE611765	HE611804	HE611844	HE611896
Jobinia streptantha (Malme) Liede & Meve	*Liede & Meve 3550* (UBT)	Ecuador: Bolivar	HE611708	HE611766	HE611805	HE611845	HE611897
Jobinia tarmensis (Schltr.) Liede & Meve	*Tupayachi & Galiano 761* (NY)	Peru: Cuzco	AJ428744	AJ428745	AJ428746	AJ699349	–
Jobinia trifurcata (Griseb.) Liede & Meve	*Liede-Schumann et al. 3636* (CORD)	Argentina: La Rioja	HE611709	HE611752	HE611752	HE611846	HE611898
Jobinia trifurcata (Griseb.) Liede & Meve	*Wood et al. 15308* (K, UBT)	Bolivia: Chuquisaca	HE611710	HE611753	HE611753	HE611847	HE611899
Jobinia umbellata (Rusby) Liede & Meve	*Goyder sub Wood 15798* (K, UBT)	Bolivia: La Paz	AJ704317	AJ704316	AJ704318	AJ704319	HE611902
Jobinia sp. indet.	*Wood & Goyder 15578* (K, UBT)	Bolivia: Santa Cruz	AJ704313	AJ704315	AJ704314	AJ704312	HE611901
Monsanima morrenioides (Goyder) Liede & Meve	*Omlor 160* (MJG)	Brazil: Bahia	AJ428684	AJ428685	AJ428686	AJ699348	HE611903
Orthosia angustifolia (Turcz.) Liede & Meve	*Nee 33059* (NY)	Mexico: Veracruz	HE611711	HE611767	HE611806	HE611848	HE611904
Orthosia angustifolia (Turcz.) Liede & Meve	*Reyes A-5219* (XAL)	Mexico: Veracruz	HE611712	HE611754	HE611754	HE611849	HE611905
Orthosia bonplandiana (Schult.) Liede & Meve	*Conrad 9306* (UBT)	Mexico: Michoacan	HE611713	HE611768	HE611807	HE611849	HE611906
Orthosia bonplandiana (Schult.) Liede & Meve	*Liede & Meve 3311* (UBT)	Venezuela: Mérida	HE611714	HE611769	HE611808	HE611851	HE611907
Orthosia bonplandiana (Schult.) Liede & Meve	*Wood et al. 13292* (K)	Bolivia: Chuquisaca	HE611715	HE611770	HE611809	HE611909	HE611908
Orthosia calycina (Schltr.) Liede & Meve	*Weigend et al. 7530* (B)	Peru: Cajamarca	HE611716	HE611755	HE611755	HE611853	HE611909
Orthosia congesta (Vell.) Decne.	*Konno 855* (SP)	Brazil: Rio de Janeiro	HE611717	HE611771	HE611810	HE611854	HE611910
Orthosia ellemannii (Morillo) Liede & Meve	*Liede & Meve 3457* (UBT)	Ecuador: Loja	AJ428780	AJ428781	AJ428782	AJ699350	HE611918
Orthosia ellemannii (Morillo) Liede & Meve	*Liede & Meve 3487* (ex hort.)	Ecuador: Carchi	HE611718	HE611772	HE611811	HE611855	HE611911

Table 1. Continued.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Orthosia ellemannii (Morillo) Liede & Meve	*Matezki 161* (UBT)	Ecuador: Loja	HE611719	HE611773	HE611812	HE611856	HE611912
Orthosia kunthii Decne.	*Hinton et al. 24347* (NY)	Mexico: Nuevo Léon	AJ428783	AJ428784	AJ428785	AJ699351	HE611919
Orthosia kunthii Decne.	*Valdés et al. 1961* (NY)	Mexico: Nuevo Léon	HE611720	HE611774	HE611813	HE611857	HE611913
Orthosia meridensis (Morillo) Liede & Meve	*Liede & Meve 3310* (UBT)	Venezuela: Barinas	HE611721	HE611775	HE611814	HE611858	HE611914
Orthosia pearcei (Rusby) Liede & Meve	*Galetto 723* (CORD, NY)	Argentina: Cordóba	HE611722	HE611776	HE611815	HE611859	HE611915
Orthosia pearcei (Rusby) Liede & Meve	*Wood 10514* (K, UBT)	Bolivia: Cochabamba	HE611723	HE611777	HE611816	–	HE611916
Orthosia pubescens (Greenm.) Liede & Meve	*Prinzie et al. 207* (TEX)	Mexico: México	HE611724	HE611778	HE611817	HE611860	HE611917
Orthosia pubescens (Greenm.) Liede & Meve	*Ventura 555* (NY)	Mexico: México	HE611725	HE611779	HE611818	HE611861	–
Orthosia scoparia (Nutt.) Liede & Meve	*Acevedo et al. 7714* (NY)	Puerto Rico	AJ704320	AJ704322	AJ704321	–	HE611920
Orthosia scoparia (Nutt.) Liede & Meve	*Axelrod 8409* (NY)	Puerto Rico	HE611726	HE611780	HE611819	HE611862	HE611921
Orthosia scoparia (Nutt.) Liede & Meve	*Easley 542* (NY)	U.S.A.: Florida	HE611727	HE611781	HE611820	HE611863	HE611922
Orthosia scoparia (Nutt.) Liede & Meve	*Mangelsdorff RMC 246* (UBT)	Cuba: Guantanamo	HE611728	HE611782	HE611821	HE611864	HE611923
Orthosia scoparia (Nutt.) Liede & Meve	*Mangelsdorff RMC 3125* (FR)	Cuba: Cienfuegos	HE611729	HE611783	HE611822	HE611865	HE611924
Orthosia scoparia (Nutt.) Liede & Meve	*van der Werff & Wingfield 7441* (NY)	Venezuela: Falcón	HE611730	HE611784	HE611823	HE611866	–
Orthosia scoparia (Nutt.) Liede & Meve	*Wasum et al. 7930* (NY)	Brazil: Rio Grande do Sul	HE611731	HE611785	HE611824	HE611867	HE611925
Orthosia scoparia (Nutt.) Liede & Meve	*Wood & Goyder 15776* (K, UBT)	Bolivia: Santa Cruz	HE611732	HE611786	HE611825	HE611868	HE611926
Orthosia scoparia (Nutt.) Liede & Meve	*Mika et al. 072* (FR)	Dominican Republic: La Vega	HE611733	HE611756	HE611756	HE611869	HE611927
Orthosia scoparia (Nutt.) Liede & Meve	*Mika et al. 073* (FR)	Dominican Republic: La Vega	HE611734	HE611787	HE611826	–	HE611928
Orthosia urceolata E. Fourn.	*Carrião 27500* (NY)	Brazil: Paraná	AJ704324	AJ704323	AJ704325	–	HE611934
Orthosia virgata (Poir.) E. Fourn.	*Morero 112* (CORD)	Argentina: Córdoba	HE611736	HE611757	HE611757	HE611871	HE611930
Orthosia woodii Meve & Liede	*Wood 10369* (K)	Bolivia: Chuquisaca	HE611737	HE611789	HE611828	HE611872	HE611931
Orthosia sp. indet. a	*Liede et al. 3640* (CORD)	Argentina: Catamarca	HE611738	HE611758	HE611758	–	HE611932
Orthosia sp. indet. b	*Wood 15994* (K, UBT)	Bolivia: Cochabamba	HE611739	HE611759	HE611759	–	HE611933
Scyphostelma beckii (Morillo) Liede & Meve	*Liede & Conrad 3141* (MSUN, ULM)	Bolivia: La Paz	AJ704305	AJ704307	AJ704306	AJ704304	–
Scyphostelma bifida (Liede & Meve) Liede & Meve	*Liede & Meve 3557* (UBT)	Ecuador: Azuay	HE611740	HE611790	HE611829	HE611873	HE611935
Scyphostelma ecuadorensis (Schltr.) Liede & Meve	*Liede & Meve 3556* (UBT)	Ecuador: Chimborazo	HE611748	HE611797	HE611836	HE611880	HE611943
Scyphostelma ecuadorensis (Schltr.) Liede & Meve	*Harling & Ståhl 26512* (S)	Ecuador: Loja	HE611741	HE611791	HE611830	HE611874	HE611936
Scyphostelma harlingii (Morillo) Liede & Meve	*Liede & Meve 3460* (UBT)	Ecuador: Zamora-Chinchipe	AJ704309	AJ704308	AJ704310	AJ704311	HE611946
Scyphostelma lechleri (Morillo) Liede & Meve	*Liede & Conrad 3136* (MSUN, ULM)	Bolivia: La Paz	AJ428753	AJ428754	AJ428755	HE611883	HE611947

Table 1. Continued.

Species	Voucher	Country	*trnT-L*	*trnL*	*trnL-F*	*rps16*	*trnD-T*
Scyphostelma microphylla (Kunth) Liede & Meve	*Cerón & Alcarón 12217* (MO)	Ecuador: Pichincha	AJ428681	AJ428682	AJ428683	AJ699347	–
Scyphostelma velutina (Morillo) Liede & Meve	*Liede & Meve 3555* (UBT)	Ecuador: Chimborazo	HE611747	HE611796	HE611835	HE611879	HE611942
Scyphostelma wurdackii (Morillo) Liede & Meve	*Liede 3342* (UBT)	Ecuador: Cuenca	HE611743	HE611793	HE611832	–	HE611938
Scyphostelma sp. indet. a	*Liede & Meve 3473* (UBT)	Ecuador: Pichincha	HE611744	HE611794	HE611833	HE611876	HE611939
Scyphostelma sp. indet. b	*Liede & Meve 3474* (UBT)	Ecuador: Pichincha	HE611745	HE611760	HE611760	HE611877	HE611940
Scyphostelma sp. indet. c	*Liede & Meve 3552* (UBT)	Ecuador: Bolívar	HE611746	HE611795	HE611834	HE611878	HE611941
Scyphostelma sp. indet. d	*Liede & Meve 3563* (UBT)	Ecuador: Loja	HE611749	HE611798	HE611837	HE611881	HE611944
Scyphostelma sp. indet. e	*Wood 10297* (K, UBT)	Bolivia: Cochabamba	HE611750	HE611799	HE611838	HE611882	HE611945
Scyphostelma sp. indet. f	*Weigend et al. 5821* (B)	Peru: Cajamarca	HE611742	HE611792	HE611831	HE611875	HE611937

South American–Central American *Orthosia* clade. These results show that neither the sampling density nor the amount of data created is yet sufficient for a species-level phylogeny of *Orthosia*. In particular, the widespread and frequent species (*O. scoparia*, *O. bonplandiana*, and, to a lesser extent, *O. ellemannii*) seem to be composed of morphologically indistinguishable but polyphyletic elements, which are more closely related to morphologically well-characterized but much more narrowly distributed species.

Clade structure in *Scyphostelma* was also difficult to reconcile to either morphological characters or geographical distributions (Fig. 1A). Three unresolved subclades were found, the first comprising *S. beckii* (Morillo) Liede & Meve (new combination herein) (*Liede & Conrad 3141*) and *Scyphostelma* sp. indet. f (*Weigend 5821*), the second comprising *S. harlingii* (Morillo) Liede & Meve (new combination herein) (*Liede & Meve 3460*) and *Scyphostelma* sp. indet. e (*Wood 10297*), and the third comprising the remainder of the *Scyphostelma* species. Only the subclade of *S. harlingii* and *Scyphostelma* sp. indet. e (*Wood 10297*) is morphologically distinct, e.g., lacking the characteristic long shoot–short shoot architecture of *Scyphostelma*.

Taxonomic Treatment

As supported by the molecular evidence presented here, the division of the Orthosiinae into three, and now a fourth and newly described, genera is warranted. These four genera, *Jobinia*, *Monsanima*, *Orthosia*, and *Scyphostelma*, are restricted to the New World and accommodate most of the diversity of former *Cynanchum* sensu Woodson (1941). All four genera are highly similar to Old World *Cynanchum*, but none of the described taxa are known to have prophylls, which therefore constitutes a synapomorphy for *Cynanchum* s. str. (as "stipules" in Liede & Täuber, 2002). In the Americas, *Cynanchum* is represented only by *Cynanchum* subg. *Mellichampia* (A. Gray) Sundell as circumscribed by Sundell (1981), which is characterized by cordate leaf bases, racemose inflorescences, and ovoid, often rather thick-walled fruits. Morphologically, the four genera of Orthosiinae remain difficult to distinguish, and the key presented here can only be used as a rough guide to the taxonomic boundaries. For a list of species names treated in this paper, see Appendix 1.

Key to the Genera of Orthosiinae

1a. Leaf blades usually not linear, but ovate or cordate, often with an extended tip, usually longer than 5 cm; inflorescences usually as long or longer than the leaves; mericarps 2, usually 5

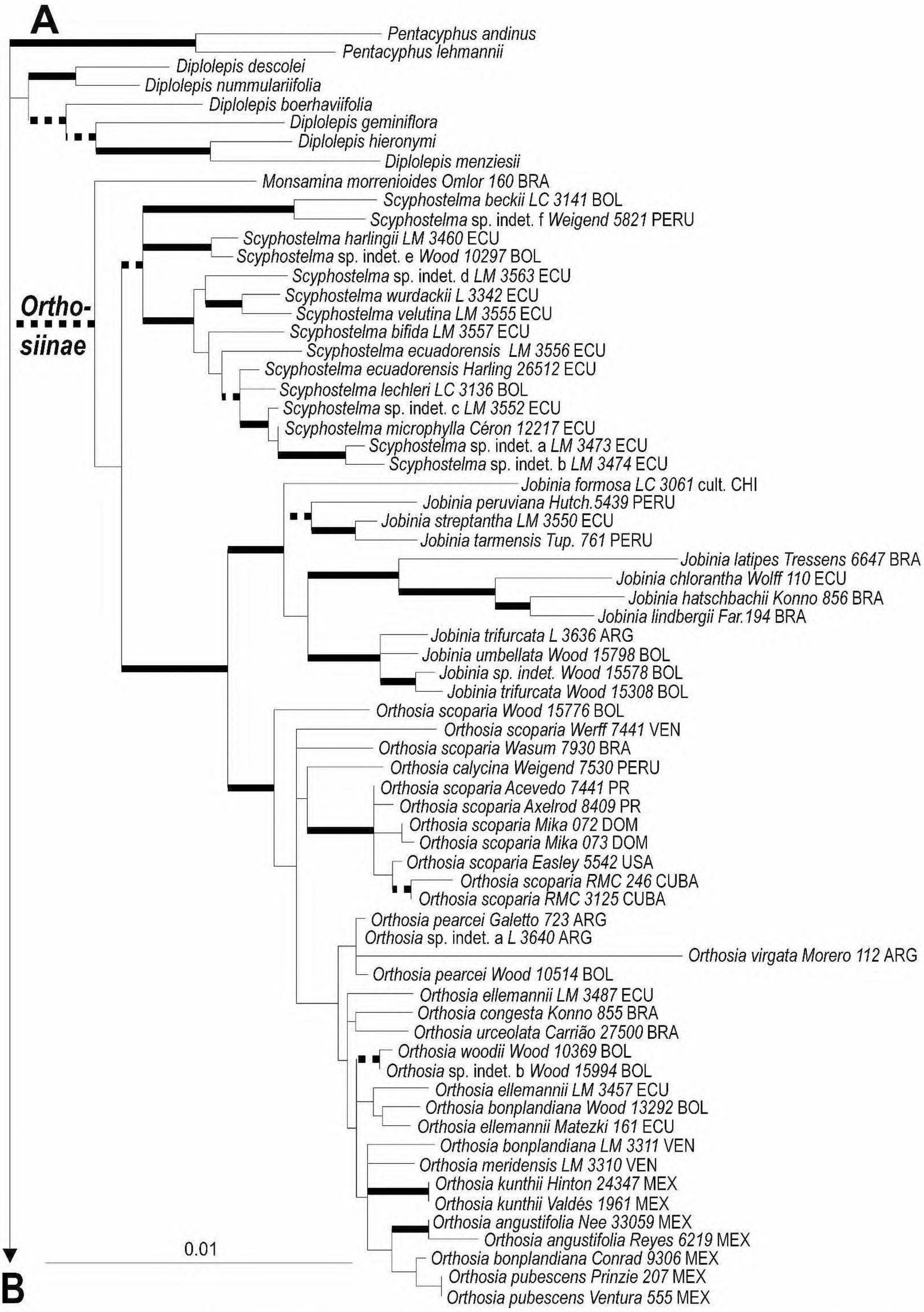


Figure 1. Tree resulting from maximum likelihood analysis (ML) of the combined dataset. Branches drawn as thick lines indicate BS values > 90% (MP and ML) and PP > 0.95 (BI); branches drawn as thick dotted lines indicate BS values 80%–89% (MP and ML) and PP > 0.95 (BI). —A. Relationships of the ingroup taxa; accessions and geographical origin indicated (see Table 1). ARG: Argentina; BOL: Bolivia; BRA: Brazil; cult. CHI: cultivated in Chile; DOM: Dominican Republic; ECU: Ecuador; MEX: Mexico; PR: Puerto Rico; VEN: Venezuela. Abbreviations of collectors used: Far.: Farinaccio; Hutch.: Hutchinson & Wright; L: Liede; LC: Liede & Conrad; LM: Liede & Meve; RMC: Mangelsdorff; Tup.: Tupayachi & Galiano (see Table 1).

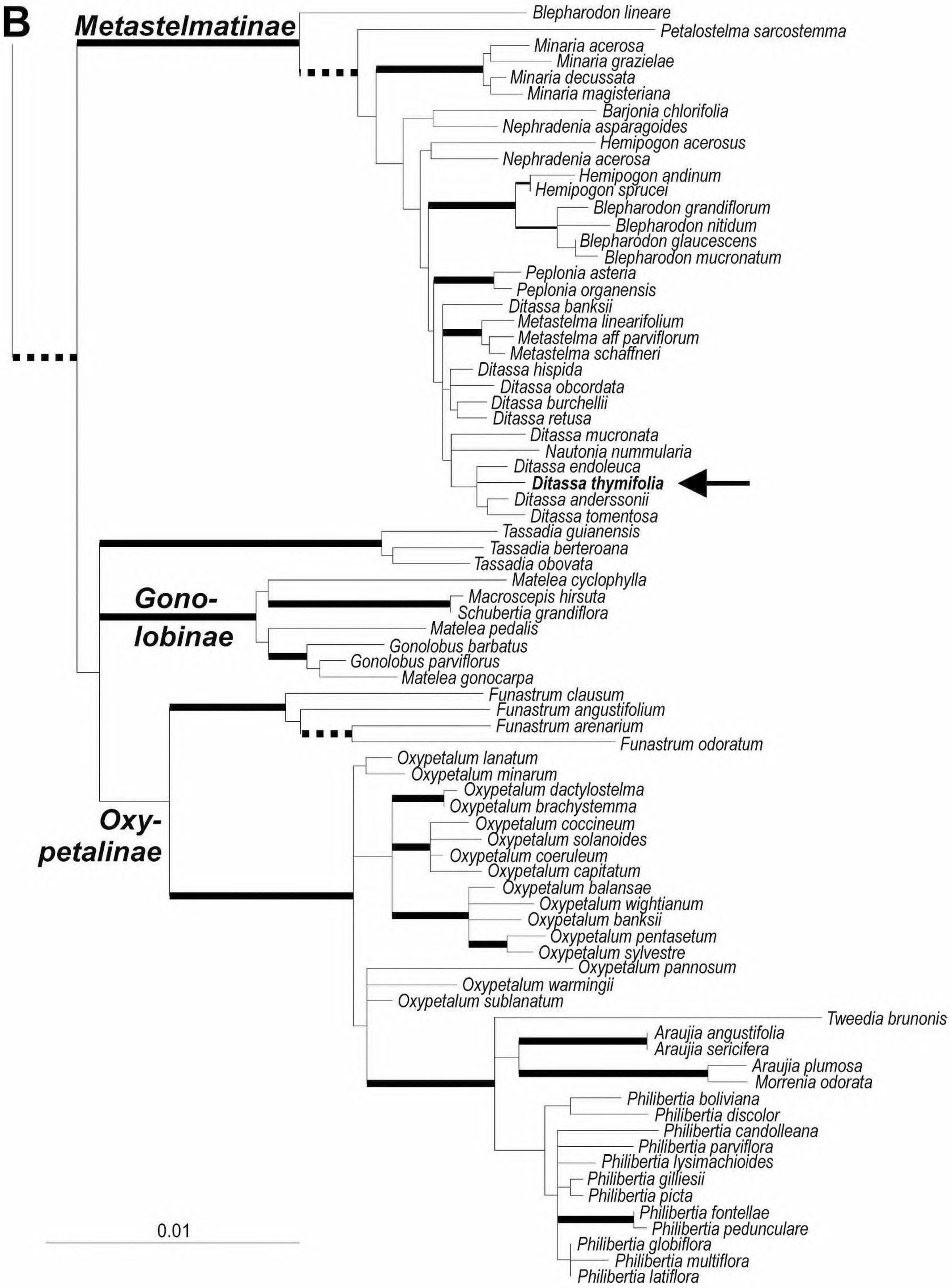


Figure 1. Continued.—B. Relationships of the outgroup taxa; partial sequences used for a species may have been produced from different accessions (see Table 1). The position of *Ditassa thymifolia* (Schltr.) Liede & Meve is indicated with an arrow.

Table 2. Sequence characteristics and models for phylogenetic analysis. Number of sequences newly reported here. The *trnD-T* spacer sequence was not analyzed across the first 250 base pairs, which were incomplete for several accessions. For several taxa, the first 243 bp of the *trnD-T* spacer were missing; for *Nephradenia asparagoides* (Decne.) E. Fourn. and *Orthosia scoparia* (Nutt.) Liede & Meve, accession *RMC 246*, 367 bp and 474 bp, respectively, were missing.

	trnT-L intergenic spacer	*trnL* intron	*trnL-F* intergenic spacer	*rps16* intron	*trnD-T* intergenic spacer
Length (bp)	747–1027	456–547	197–387	738–849	914–1321 (989–1184)
Aligned length (bp)	1235	587	443	927	1592
New sequences	49	49	49	45	64
Missing partial sequences	0	0	0	6	63
Missing data (% total)	0.2	0.3	0.7	4.7	total: 47.6; ingroup: 20.9
Missing data (% in available partial sequences)	0.2	0.3	0.7	0.6	9.3
Variable characters	272	87	100	232	252
Parsimony informative characters	119	38	44	114	108
Best-fit model of nucleotide substitution (24 models tested)	GTR	GTR+G (AIC, BIC); HKY+G (AICc)	GTR+G (AIC, BIC); F81+G (AICc)	GTR+G	HKY+I+G (AIC, AICc) F81+I+G (BIC)
Best-fit model of nucleotide substitution (88 models tested)	TVM+G	trN+G	TIM1+G (AIC, BIC); F81+G (AICc)	TVM+G	HKY+I+G (AIC, AICc) F81+I+G (BIC)

Abbreviations: AIC: Akaike information criterion; AICc: Akaike information criterion corrected for small datasets; BIC: Bayesian information criterion; F81: Felsenstein (1981); GTR: general time reversible model (Tavaré, 1986); HKY: Hasegawa-Kishino-Yano (1985); TIM: transitional model: rAC = rGT ≠ rAT = rCG ≠ rAG ≠ rGT; TrN: Tamura & Nei (1993); TVM: transversional model: rAC = rCT ≠ rAG ≠ rAT ≠ rCG ≠ rGT; +G: shape parameter of the gamma distribution accounting for substitution rate heterogeneity; +I: proportion of invariant sites.

cm or longer, at acute angles, occasionally remaining fused at the tips ..... I. *Jobinia*

1b. Leaf blades linear to lanceolate, if other shapes, then distinctly shorter than 5 cm; inflorescences usually shorter than the leaves; mericarps 1 or 2, usually < 5 cm long, at various angles, but never fused at the tips 2

2a. Anther wings not extending the entire length of the anther, basally strongly centrifugal; corona united into a tube obscuring the gynostegium; tube folded inward apically ..... II. *Monsanima*, new genus

2b. Anther wings usually extending the entire length of the anther, never strongly centrifugal basally; corona either not united into a tube obscuring the gynostegium, or, if so, then the tube not folded inward apically 3

3a. Inflorescences often axillary or almost so, stems green, long and short shoots not conspicuously distinct, often leafless at flowering time; mericarps always in pairs at obtuse angles, ± cylindrical without distinct beak ..... III. *Orthosia*

3b. Inflorescences usually not axillary, stems usually soon turning brown, long and short shoots usually conspicuously distinct, if indistinct, then stems not green; leaves occasionally not linear, but rarely longer than 2 cm (those on short shoots always shorter); mericarps single or paired, at various angles, distinctly fusiform or spindle-shaped and often beaked ..... IV. *Scyphostelma*

ORTHOSIINAE

I. Jobinia E. Fourn., Flora Brasiliensis 6(4): 327, pl. 97. 1885. TYPE: *Jobinia hernandiifolia* (Decne.) E. Fourn.

Cyathostelma E. Fourn., Flora Brasiliensis 6(4): 219. 1885, syn. nov. TYPE: *Cyathostelma latipes* (Decne.) E. Fourn. [≡ *Metastelma latipes* Decne., ≡ *Jobinia latipes* (Decne.) Liede & Meve].

Dicarpophora Speg., Physis (Buenos Aires) 8: 269. 1926, syn. nov. TYPE: *Dicarpophora mazzuchii* Speg. [≡ *Cynanchum mazzuchii* (Speg.) Liede].

Jobinia was established by Fournier (1885) with two species from Brazil, the generitype *J. hernandiifolia* (Decne.) E. Fourn. and *J. lindbergii*. The extended key of Fontella Pereira and Schwarz (1982) would later recognize an additional three species in Brazil: *J. hatschbachii*, *J. lutziae* Fontella & E. A. Schwarz, and *J. paranaensis* Fontella & C. Valente. In their treatment (Fontella Pereira & Schwarz, 1982), *J. hernandiifolia* was transferred to synonymy of *J. connivens* (Hook. & Arn.) Malme, and *J. furcata* (E. Fourn.) Fontella as a synonym to *J. lindbergii*. One species from Ecuador and Bolivia, *J. chlorantha*, is listed but not further treated. To these six species, Stevens (2000) added two from Ecuador, *J. balslevii* (Morillo) W. D. Stevens (Fig. 2) and *J. campii* (Morillo) W. D. Stevens, and one more, *J. eulaxiflora* (Lundell) W. D. Stevens, from Guatemala in Central America. Liede and Meve (2001) further described a Venezuelan taxon, *J. neei* (Morillo) Liede & Meve, as well as one from Argentina, *J. glossostemma* (Lillo) Liede & Meve. Fontella Pereira and Britto de Goes (2007) subsumed *J. lutziae* under *J. grandis* (Hand.-Mazz.) Goes & Fontella, resolving the issue of an unusually large-flowered *Orthosia*, and described one more Brazilian species, *J. longicoronata* Goes & Fontella, which brought the recognized generic total to 12 species, of which six are from Brazil. Two of these established taxa, *J. hatschbachii* and *J. lindbergii*, were represented in the phylogenetic analysis by Brazilian accessions, and both are well embedded within the larger *Jobinia* clade, affined to a *J. chlorantha* accession from Zamora-Chinchipe, Ecuador.

Herein, 13 more species are added to the genus, 12 of which are transferred from *Cynanchum*. One species, *Jobinia peruviana*, is new to science, and is highly atypical for *Jobinia*, with its erect habit, linear leaves, and depauperate inflorescences. However, the molecular analysis is unambiguous as to the position of this species within *Jobinia*. Of the 25 species of the genus, eight now come from Brazil, whereas 13 are found in the high Andes of Ecuador, Peru, and Bolivia. Especially in Bolivia, more species might await description following a more detailed study, as the one unnamed collection included in the molecular study (*Wood 15578*) indicates. The range of two species extends south into Argentina, one north to Venezuela, and one more reaches Central America in Guatemala. Most of the species are rare in their distributions and occur in very small populations; often only a single individual is found over a quite large distance (Liede-Schumann & Meve, pers. obs.).

The inclusion of *Dicarpophora*, which was lectotypified by Liede (1997), is based on the figure from Spegazzini's 1926 protologue, because all attempts to trace material from Spegazzini failed. The plant depicted, however, shows the often heart-shaped leaves; the richly branched, loose inflorescences (e.g., *Jobinia balslevii*, Fig. 2); and the long, almost parallel fruits of *Jobinia* (e.g., *J. canoi* (Morillo) Liede & Meve, Fig. 3). However, it cannot be ascertained whether another similar one of the recognized *Jobinia* species is depicted, and Spegazzini's statement that it was sent to him from a garden in Tupiza (Bolivia) likewise gives no useful hint to its identity. Therefore, it seems prudent to continue to recognize *J. mazzuchii* (Speg.) Liede & Meve as a separate species. Additionally, with the inclusion of both species of *Cyathostelma*, *C. furcatum* E. Fourn. and *C. latipes*

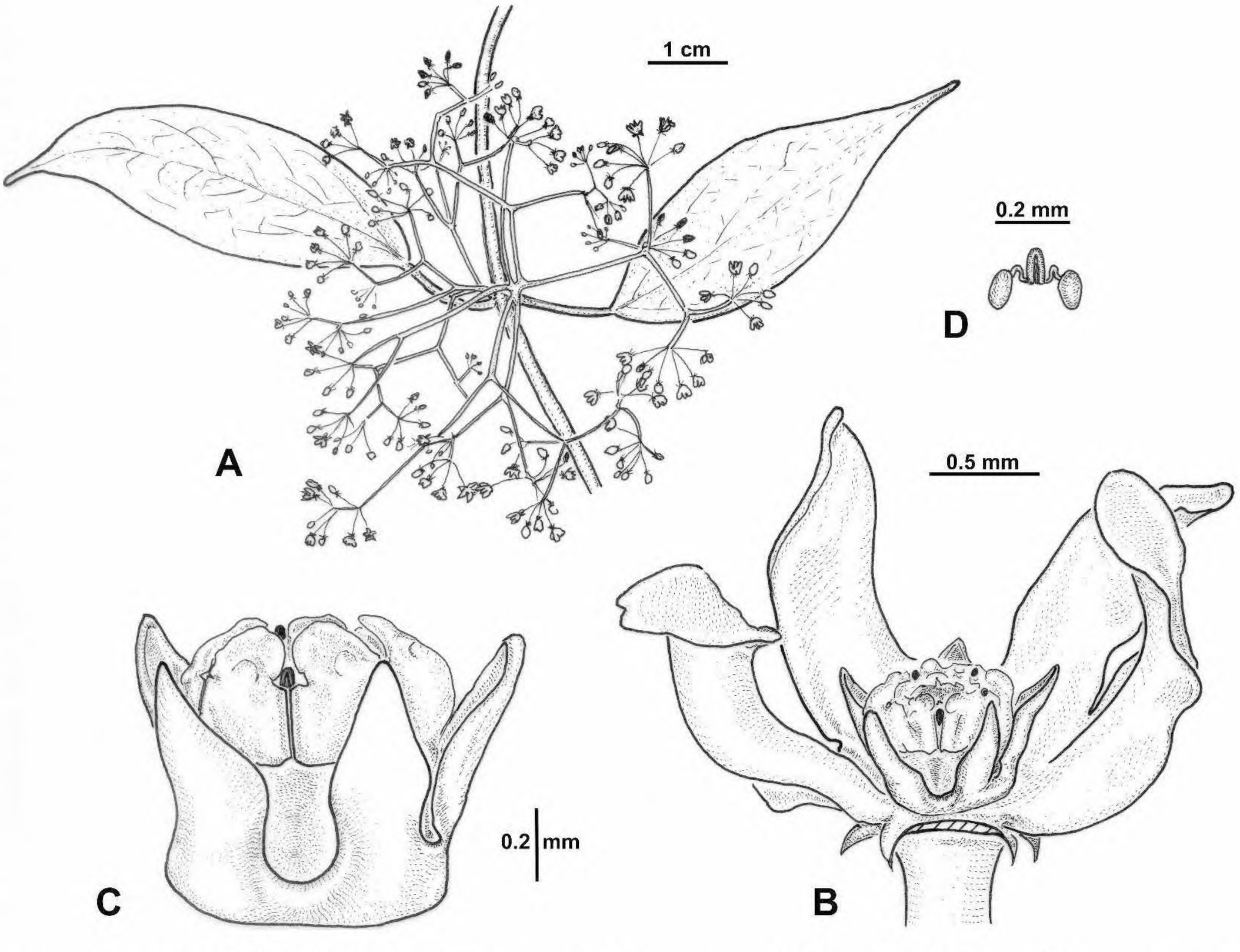


Figure 2. *Jobinia balslevii* (Morillo) W. D. Stevens. —A. Inflorescence. —B. Flower, lateral view. —C. Gynostegium and corona. —D. Pollinarium. A–D from isotype *Balslev 10415* (NY). Drawn by U. Meve.

(Decne.) E. Fourn., in *Jobinia*, no component species remain for the genus *Cyathostelma* sensu Fournier (1885).

Included species. The 25 taxa of *Jobinia* are listed here; those included in the molecular analysis are indicated in boldface. *J. balslevii* (Morillo) W. D. Stevens, *J. campii* (Morillo) W. D. Stevens, *J. canoi* (Morillo) Liede & Meve [≡ *Cynanchum canoi* Morillo], ***J. chlorantha*** (K. Schum.) Malme, *J. connivens* (Hook. & Arn.) Malme, *J. eulaxiflora* (Lundell) W. D. Stevens, *J. fontellana* Liede & Meve [≡ *Orthosia hatschbachii* Fontella & Goes], ***J. formosa*** (N. E. Br.) Liede & Meve [≡ *C. formosum* N. E. Br.], *J. glossostemma* (Lillo) Liede & Meve, *J. grandis* (Hand.-Mazz.) Goes & Fontella, ***J. hatschbachii*** Fontella & E. A. Schwarz, ***J. latipes*** (Decne.) Liede & Meve [≡ *Metastelma latipes* Decne.], ***J. lindbergii*** E. Fourn., *J. longicoronata* Goes & Fontella, *J. mazzuchii* (Speg.) Liede & Meve [≡ *Dicarpophora mazzuchii* Speg.], *J. neei* (Morillo) Liede & Meve, *J. paranaensis* Fontella & C. Valente, ***J. peruviana*** Liede & Meve, *J. samuelssonii* (Malme) Liede & Meve [≡ *C. samuelssonii* Malme], *J. schizocorona* (Liede & Meve) Liede & Meve [≡ *C. schizocoronum* Liede & Meve], ***J. streptantha*** (Malme) Liede & Meve [≡ *C. streptanthum* Malme], ***J. tarmensis*** (Schltr.) Liede & Meve [≡ *C. tarmense* Schltr.], *J. tiarata* (Malme) Liede & Meve [≡ *C. tiaratum* Malme], ***J. trifurcata*** (Griseb.) Liede & Meve [≡ *Metastelma trifurcatum* Griseb.], ***J. umbellata*** (Rusby) Liede & Meve [≡ *Vincetoxicum umbellatum* Rusby].

1. Jobinia canoi (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum canoi* Morillo, Ernstia 4: 4. 1994. TYPE: Peru. Cusco: Paucartambo, Acjanaco, Parque Nac. Manú, Trocha Ericsson, 3350–3400 m, 27 Mar. 1992, *A. Cano E. 5365* (holotype, USM!; isotype, MERF!). Figure 3.

Morphological evidence clearly points to *Jobinia* for generic affiliation of *Cynanchum canoi*. First of all the species possesses a highly significant and key character of *Jobinia*, the fusiform and parallel to sparsely spreading two mericarps, whereas in *Scyphostelma* and *Cynanchum* only single mericarps are formed. In *Orthosia*, two mericarps are also the rule; however, these are narrowly oblong, spreading, and smooth (and also never longitudinally grooved as in parts of *Jobinia*, including *J. canoi*, Fig. 3F). Vegetatively, *J. canoi* is hard to distinguish, e.g., from *J. chlorantha* or *J. hatschbachii*, with its glabrous (or nearly so) leaves of smooth and thin texture. Rostrate style heads are found in quite a number of *Jobinia* species, e.g., *J. peruviana* (Fig. 4)

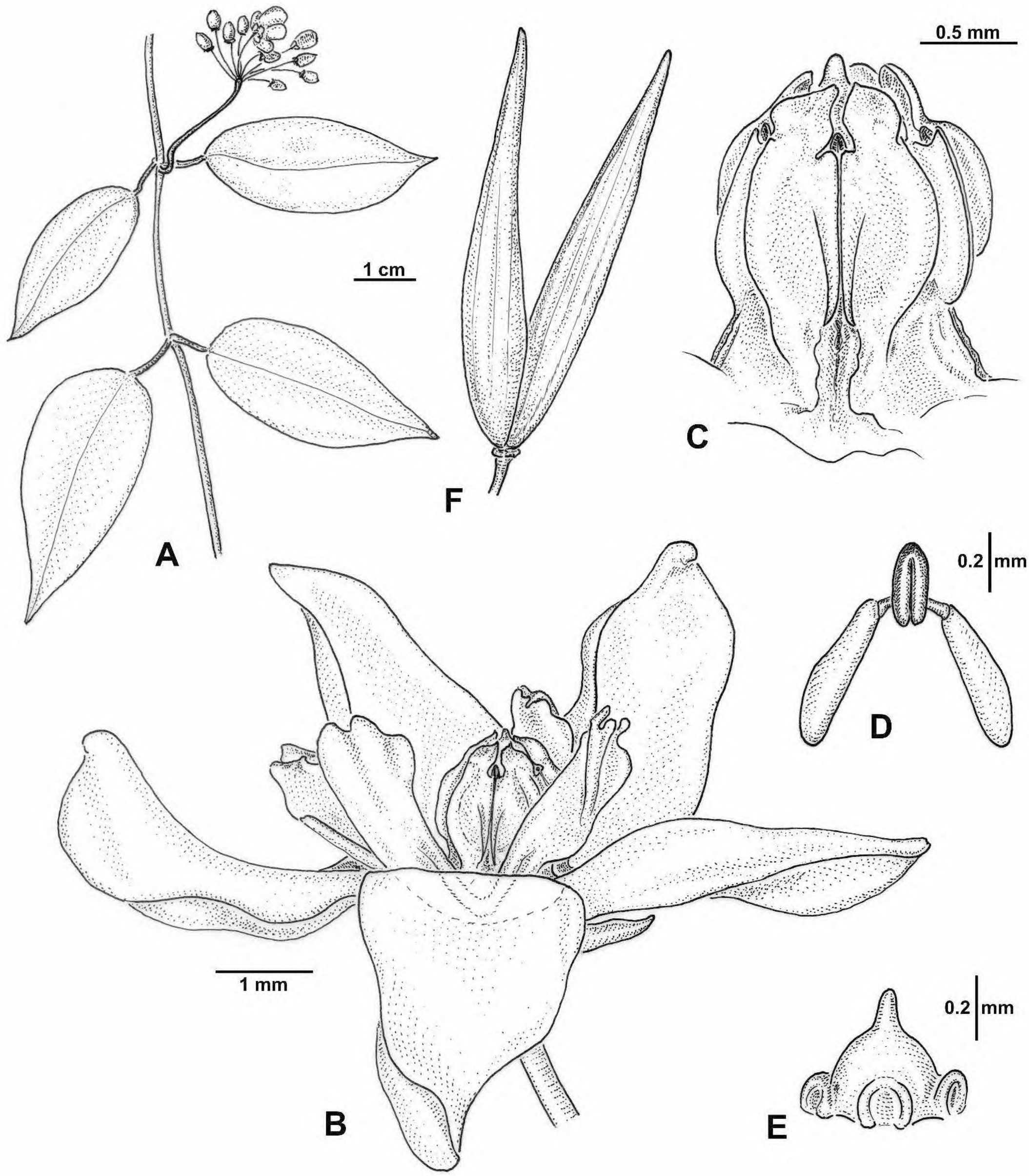


Figure 3. *Jobinia canoi* (Morillo) Liede & Meve. —A. Branch with inflorescence. —B. Flower, lateral view. —C. Gynostegium. —D. Pollinarium. —E. Style head. —F. Twin mericarps. A–F from *Herrera 2086* (S). Drawn by U. Meve.

or *J. streptantha*, but this feature is not known from New World *Cynanchum* or *Orthosia*.

The type specimen of *Jobinia canoi* is a leafless tangle of green shoots with flowers too large for an *Orthosia*. However, two more specimens were discovered, one, *Herrera 2086* (Fig. 3), showing both well-developed leaves and the typical rather large (to 7 cm), slightly spreading two mericarps of *Jobinia*. We were unable to sequence an accession from this scant material to further address its relationships.

Additional specimens examined. PERU. **Ancash Region:** Carhuaz Distr., Huascarán Nat. Park, Quebrada Honda, valley bottom, 9°19′S, 77°28′W, 3600–3800 m, *Smith et al. 11689* (USM). **Ucayali:** Calca, Valle de Urobamba, 3000 m, *Herrera 2086* (S).

2. Jobinia chlorantha (K. Schum.) Malme, Ark. Bot. 25A(7): 3–4, tab. 2 & 3. 1932. Basionym: *Roulinia chlorantha* K. Schum, Bot. Jahrb. Syst. 25: 729. 1898. TYPE: Ecuador. Zamora-Chinchipe: Est. Cien. San Francisco, shortcut from

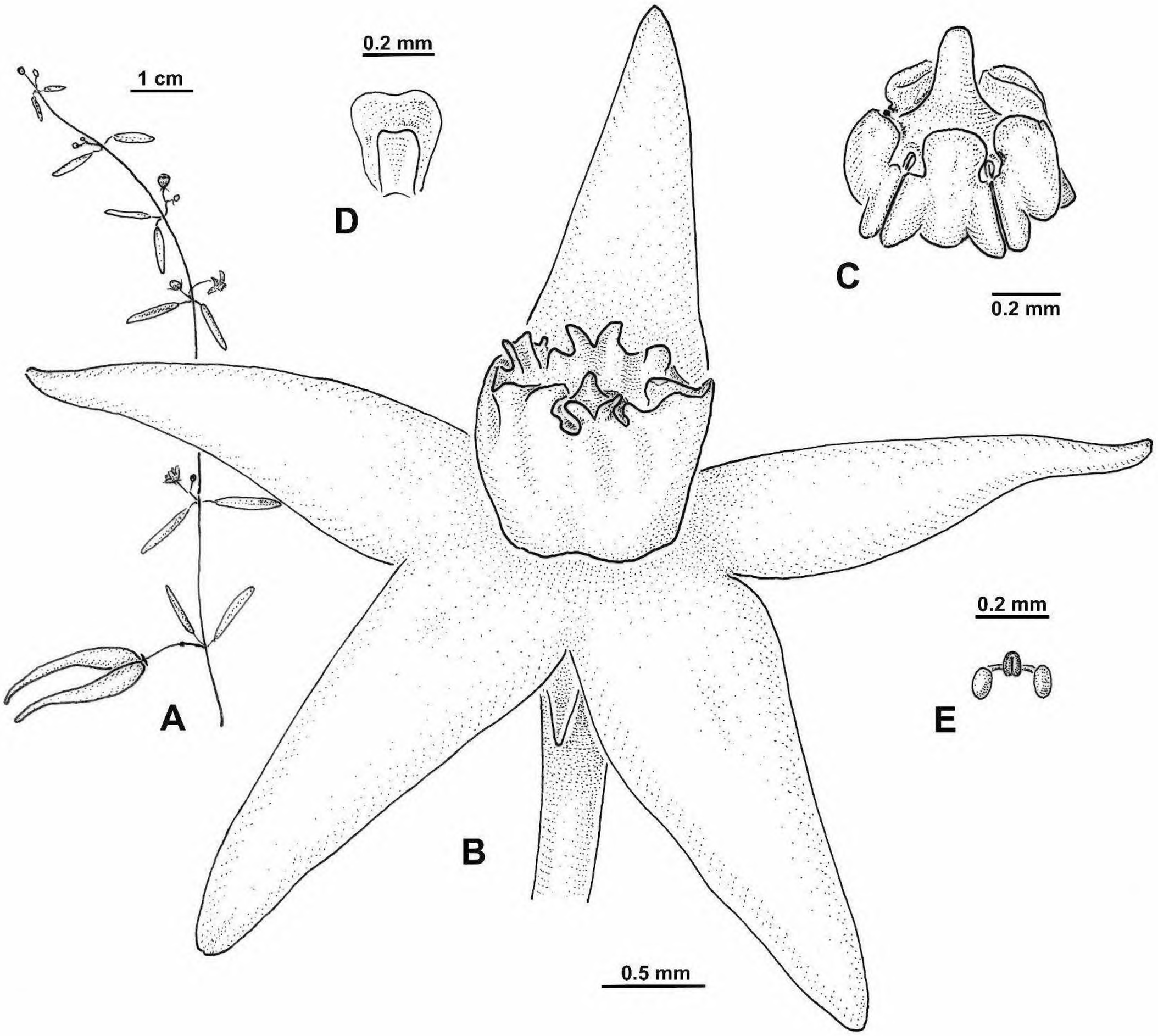


Figure 4. *Jobinia peruviana* Liede & Meve. —A. Plant with twin mericarps. —B. Flower, lateral view. —C. Gynostegium. —D. Corona lobe, adaxial view. —E. Pollinarium. A–E from holotype *Hutchinson & Wright 5439* (S). Drawn by U. Meve.

tarabita to path along channel, alt. 1850 m, 17 Feb. 2000, *S. Matezki 169* (neotype, designated here, UBT!). Figure 10B.

The type specimen of *Jobinia chlorantha* dates back to the end of the 19th century (Schumann, 1898, as *Roulinia chlorantha* K. Schum.) and the collecting activities of L. Sodiro (*Sodiro 107/2*) on the Pichincha in the vicinity of Quito, Ecuador. The holotype as well as one additional specimen from there, *Sodiro 107/8* (photo in F), were housed in B and probably destroyed by the fire in 1942. Since then, this species has not been recollected in Ecuador. It was up to S. Matezki (*Matezki 169*) in 2000 and later D. Wolff (*Wolff 110*), in the course of research projects on vines and the reproductive biology of Rubiaceae and Asclepiadoideae in southern Ecuador, to relocate this species in the country after more than 100 years (Wolff et al., 2008). In choosing a neotype, we concentrated on these collections that originate from the same country as the lost holotype, and finally selected *Matezki 169* because this collection is represented in UBT by a flowering exsiccate as well as a spirit collection. The studies of Wolff et al. (2008) also yielded the first pollination observations for a *Jobinia* species, establishing that *J. chlorantha* is (predominantly) pollinated by small wasps (Ichneumonidae). In our molecular phylogeny (Fig. 1), *J. chlorantha* falls in the "Brazilian" clade. Considering floral morphology, this very small-flowered species is quite distinct from the remaining three species of the clade (see discussion under *J. latipes*). However, it shares with *J. lindbergii* the distinct ovate-elliptic corpuscles, bent and filiform caudicles, and ovoid pollinia.

Additional specimens examined. ECUADOR. **Zamora-Chinchipe:** Est. Cien. San Francisco (ca. 30 km E from

Loja), 20 Oct. 2001, *Wolff 110* (UBT); Est. Cien. San Francisco (ca. 30 km E from Loja), near the tarabita, 5 Oct. 2000, *Liede & Meve 3466b* (UBT).

3. Jobinia fontellana Liede & Meve, nom. nov. Replaced synonym: *Orthosia hatschbachii* Fontella & Goes, Revista Biol. Neotrop. 1(1–2): 1. 2004 [2005] non *Jobinia hatschbachii* Fontella & E. A. Schwarz, Bol. Mus. Bot. Munic. 51: 8–9, fig. 5–7. 1982. TYPE: Brazil. Paraná: Laranjeiras do Sul, Campo Novo, 8 June 1968, *G. Hatschbach & O. Guimarães 19295* (holotype, MBM not seen; isotypes, CTES not seen, MO-2878860!).

Morphologically, *Jobinia fontellana* shares characters with *J. latipes* and *J. hatschbachii*. However, it lacks the short and winged petioles and the pilose anthers of *J. latipes*, and its flowers maximally reach half the size of those of *J. latipes*. *Jobinia hatschbachii* has a yellow and shortly pilose corolla, whereas the corollas of *J. fontellana* and *J. latipes* are creamish or greenish and glabrous. In addition, the corona of *J. hatschbachii* is broader than long (< 1.5 mm), and apically nearly fused, obscuring the gynostegium, whereas in *J. fontellana* and *J. latipes* the corona is longer than broad (> 2 mm) but not as highly fused and not obscuring the gynostegium (Fontella Pereira & Britto de Goes, 2004).

4. Jobinia formosa (N. E. Br.) Liede & Meve, comb. nov. Basionym: *Cynanchum formosum* N. E. Br., Bull. Misc. Inform. Kew 1895: 112. 1895. TYPE: Peru. Arequipa, Apr. 1863 (fl., fr.), *M. Guillaume s.n.* (lectotype, designated here, K [barcode] 000195460!; isolectotype, K [barcode] 000197153!).

Cynanchum ecuadorense Schltr., Bot. Jahrb. Syst. 34 (Beibl. 78): 15–16. 1904. TYPE: Ecuador. In silvis vulc. Pululahua, *Sodiro 107/16* (lectotype, designated here, G [barcode] 00039950!).

Cynanchum eurystephanum Malme, Ark. Bot. 25A(7): 7–8, fig. 6. 1932. TYPE: Peru. Lima: prope Viscas 2000–2300 m, June 1925, *F. W. Pennell 14440* (holotype, S!; isotypes, NY!, US not seen).

Of the seven syntypes listed for *Cynanchum formosum* (*McLean s.n.*, K [barcode] 000197152!; *Carson s.n.*, K [barcode] 000197151!; *Guillaume s.n.*, K [barcode] 000195459!; *Guillaume s.n.*, K [barcode] 000195460!; *Pearce 84*, K [barcode] 000195454!; *Pearce s.n.*, K [barcode] 000195455!; *Pavon s.n.*, K [barcode] 000195450!), *Guillaume s.n.* (K [barcode] 000195460) was selected as lectotype, because it shows both flowers and fruits. According to label information, the specimen was raised at Kew from seeds received from M. Guillaume.

Schlechter (1904: 16) cites two subsequent Sodiro specimens as syntypes for *Cynanchum ecuadorense*: "[c]rescit in silvis subandinis montis ingivomi Pululahua (S. n. 107/15 et n. 107/16)." Neither specimen was encountered in B, but a specimen of *Sodiro 107/16* was encountered in G. Affixed to the specimen there is a label stating "Lectotipo de *Cynanchum ecuadorense* Schlechtr. G. Morillo, 1985." However, the lectotypification was never published. To honor Morillo's work and to avoid confusion, this specimen is selected as lectotype here.

Jobinia formosa is certainly the most widespread and frequent of all *Jobinia* species. Due to its rambling growth and luxuriant inflorescences, the taxon is often cultivated, and therefore its original distributional area is difficult to identify. However, all known collections come from Ecuador and Peru, so that it has to be considered an Andean species. The plant used for sequencing (Table 1) was found in a neglected garden along the Chilean coast, which is most likely outside the natural range of the species, since the species has never been reported from Chile or from coastal habitats. *Jobinia formosa*, while clearly a member of the *Jobinia* clade, took an isolated position in this clade. An additional specimen from the natural habitat of the species would ascertain this position.

Additional specimens examined. ECUADOR. **Chimborazo:** Interandine highland, Riobamba, *Rimbach 675* (NY); NE Riobamba, *Schimpff 742* (G, MO). **Guayaquil:** Huayaquil, *Pavon s.n.* (syntype, *Jobinia formosa*, K [barcode] 000197150). **Loja:** Loja, *Asplund 18114* (B, NY, R). **Pichincha:** In silvis prope Niebly, *A. Sodiro 107/15* (syntype, *Cynanchum ecuadorense*, QCNE); Niebly, *Sodiro 107b* (Q). PERU. s. loc. *J. McLean s.n.*, (syntype, *J. formosa*, K [barcode] 000197152). **Ancash:** Huaylas, 3.3 km SE of Pto. Pobre, ca. 27 km NW of Yungay, along Rio Santa, *Stevens 21977* (NY). **Arequipa:** 1855, *Carson s.n.* (syntype, *J. formosa*, K [barcode] 000197151). **Ayacucho:** Huanta prov., above Huanta, Apr. 1867, *R. Pearce s.n.* (syntype, *J. formosa*, K [barcode] 000197155). **Cajamarca:** Contumaza, carr. Cascas–El Chorrillo 07°30′S, 078°47′W, 1400 m, 22 Aug. 1994, *Merello et al. 1055* (M, MO); Sangal (San Pablo), 2000 m, *Sagástegui et al. 15365* (MO, NY). **Huánuco:** Huánuco, *Pearce s.n.* (syntypes, *J. formosa*, K [barcode] 000197153, K [barcode] 000197154). **Lima:** NE of Huinca, Santa Eulalia Rd., 11°50′S, 076°40′W, 2350–2450 m, *Gentry & Smith 36123* (AAU, MO, NY); Canta Rd. to Canta, Km. 74 near Yasoa to outside of Canta, 11°30′S, 076°45′W, 1800–2500 m, *Sullivan et al. 958* (MO, NY); Huarochirí, just above Matucana, Km. 80 on carr. Central, *Ugent & Ugent* 5301 (WIS); vic. of Matucana, *Rose & Rose 18666* (NY); Km. 72 on carr. Central betw. Lima & Oroya, 2000 m, *Stevens 22100* (GA, MO, NY); along slopes of carr. Central toward Lima, 11°50′S, 076°25′W, 2900–4100 m, *Sullivan et al. 1109* (MO, NY); S of Matucana along carr. Central, 11°50′S, 076°20′W, 2000–3000 m, *Sullivan et al. 864* (NY). **Otuzco:** La Libertad, Cascasday (Collambay–

Sinsicap), *Sagástegui et al. 15646* (MO, NY). **Moquegua:** Prov. General Sánchez Cerro rd. from Amate to San Francisco, above Omate, hillsides of Urimalle, 1840 m, *Ackermann & Cáceres 678* (M).

5. Jobinia latipes (Decne.) Liede & Meve, comb. nov. Basionym: *Metastelma latipes* Decne., Prod. 8: 513. 1844. *Cyathostelma latipes* (Decne.) E. Fourn., Fl. Bras. 6(4): 219. 1885. *Orthosia latipes* (Decne.) Malme, Svensk Bot. Tidskr. 22: 53. 1928. TYPE: Brazil. s.d., *C. F. P. von Martius s.n.* (holotype, M!).

Jobinia latipes, *J. hatschbachii*, *J. lindbergii*, and *J. chlorantha* form a very well-supported clade (MP/ML: 100% BS, BI: 1.0 PP), and *J. latipes* is retrieved, equally well supported, in sister group position to the remaining taxa. Except for *J. chlorantha*, an Ecuadorian species, the other three taxa come from southern Brazil and northern Argentina. However, the group is not yet sufficiently studied to understand the geographic patterns involved. Vegetatively, all four species representing this "Brazilian" subclade of *Jobinia* (Fig. 1) are fairly similar, sharing glabrous, elliptic, (sub)coriaceous leaves of very smooth surface and texture. The group is characterized by the formation of two (rarely three) conspicuously short and thick colleters at the base of the lamina, a character already mentioned by Fournier (1885) in the protologue of *J. latipes*. However, *J. latipes* is clearly distinct from the other species in the clade by the flattened, slightly winged petioles, to which the epithet "latipes" refers. These petioles are much shorter (10–20 mm long in material from Brazil [Malme, 1928], and only 6.5 mm long in Argentina [*Tressens et al. 6647*, UBT]) than the petioles in the other three species of the clade. Floral structure, in contrast, is rather variable in this clade. In most species, the corona surrounds the gynostegium, but in *J. chlorantha*, the strongly folded corona completely obscures a short stipe, so that the gynostegium appears to sit on top of the corona (Fig. 10B). Boletus-shaped style heads are characteristic for this clade, while the shortly pilose anthers (Fig. 10C) of *J. latipes* constitute a unique apomorphy within Asclepiadeae as a whole.

Additional specimen examined. ARGENTINA. **Corrientes:** Predio Guarani, 26°56′S, 054°15′W, 16 Oct. 2000, *Tressens et al. 6647* (CTES, UBT).

6. Jobinia mazzuchii (Speg.) Liede & Meve, comb. nov. Basionym: *Dicarpophora mazzuchii* Speg., Physis (Buenos Aires) 8: 270–271. 1926. *Cynanchum mazzuchii* (Speg.) Liede, Novon 7(2): 175. 1997. TYPE: Bolivia. Tupiza: Cult in horto Domini O. Reyes, Mar. et May 1926, *A. Mazzuchi s.n.* (lectotype, designated by Liede [1997: 175]; unnumbered figure in Spegazzini [1926: 271]).

Discussion. The single species of the genus *Dicarpophora* clearly represents a *Jobinia*, resembling closely *J. formosa* with its almost parallel twin mericarps, long-pedunculate inflorescences, and ovate, basally cordate leaves. As no extant material has been found and the quality of the photograph chosen as lectotype does not permit a close examination of the flower, it seems best to continue the recognition of this species.

7. Jobinia peruviana Liede & Meve, sp. nov. TYPE: Peru. Cajamarca: Celendin, Río Marañon opposite Balsas, river cliffs, ca. 800 m, 29 May 1964, *P. C. Hutchinson & J. K. Wright 5439* (holotype, S!; isotype, USM!). Figure 4.

Haec species a congeneris habitu humili fruticoso haud volubili, foliis parvis anguste ellipticis, inflorescentia depauperata atque floribus parvis distinguitur.

Plants erect to ascending, non-twining shrubs, to 50 cm high, sparsely branched, glabrous all over; shoots herbaceous, basally woody, with grayish bark; internodes 1.5–3 cm, 0.5–1.2 mm diam. Leaves with the petiole 1–2 mm, colleters absent; leaf blades 8–14 × 1.4–1.7 mm, narrowly elliptic, basally cuneate, apically obtuse, minutely mucronate, lateral veins seemingly absent. Inflorescences sciadioidal, 1- to 4-flowered, 1 or 2 flowers open synchronously, (sub)sessile to very shortly (–2 mm) pedunculate; floral bracts ca. 0.3 × 0.15 mm at the base, lanceolate, cream, abaxially glabrous, smooth; pedicels 2.5–3.5 mm, glabrous; floral buds ca. 2 mm, ca. 1.2 mm diam., ovoid. Calyx entirely free to basally fused, rotate, abaxially glabrous, with 2 colleters in sinuses, lobes ca. 1 × 0.4 mm, slenderly elliptic, apically acute; corolla rotate, ca. 3.5 × 5.5 mm; corolla lobes basally fused or fused to ca. 1/4 corolla length, ca. 1 mm wide, slenderly triangular, apically acute, horizontal to declined, abaxially yellow to greenish yellow (chartreuse, fide *Hutchinson & Wright 5439*); gynostegial corona tubular, of almost completely fused staminal lobes, ca. 1.2 mm, equaling the gynostegium, upper margin plicate, emarginate, lobes trilobate, erect, with a conspicuous adaxial thickening in staminal position and forming a pouch in interstaminal position; gynostegium ca. 0.5–0.6 long, ca. 0.5 mm diam., about as long as broad, sessile, conical; anthers ca. 200 μm, wider than long, abaxially gibbous and slightly basally arched, anther wings ca. 200 μm, extending the length of the anther,

at a ca. 25° angle, in the same plane as anther; connective appendages ca. 160 × 160 μm, broadly deltate, slightly inflexed; corpusculum ca. 65 × 50 μm, broadly ovoid; caudicles ca. 40 μm, straight, horizontal, attached at ca. 1/2 of corpusculum length; pollinia subapically attached to the caudicles, ca. 85 × 50 μm, ellipsoid, vertical; style head ca. 500 × 500 μm diam., upper portion ca. 300 μm, longer than the lower part, ob-infundibuliform, and apically slightly bifurcate. Follicles normally 2 per flower, with a sharp angle between them, horizontal to erect, to 30 × 3 mm, obclavate, apically strongly beaked, light brown, glabrous.

Phenology. *Jobinia peruviana* was collected in flower and with fruits in May.

Discussion. *Jobinia peruviana* is known only from the type collection. The new species is a rather atypical *Jobinia* because of its small, shrubby habit; small, narrowly elliptic leaves; and depauperate inflorescences with small flowers. Yet, molecular analysis places it clearly in *Jobinia* (Fig. 1), affined with a Peruvian accession of *J. streptantha* and an Ecuadorian accession of *J. tarmensis* (MP/ML: 88%/89% BS and BI: 0.99 PP), both species with morphologies more typical of the genus.

8. Jobinia samuelssonii (Malme) Liede & Meve, comb. nov. Basionym: *Cynanchum samuelssonii* Malme, Ark. Bot. 26A(4): 21–22. 1933. TYPE: Argentina. Tucumán: Dept. Francas, Pico de la Cuesta, ca. 1700 m, Apr. 1926, *S. Venturi 4439* (holotype, S!; isotype, MO not seen, MO-1232935 digital image!). Figure 5.

Apparently, this species has been collected only once. Its large, glabrous leaves (3–5[–6.5] × 2–3 [–4.5] cm), multiflowered inflorescences, fused corona, and rostrate style head place it clearly in *Jobinia*. Meyer (1944: fig. 69) published a full-page lithograph of the type plant (sub *Cynanchum samuelssonii*) in Descole's monumental treatment of Argentinean Asclepiadoideae.

9. Jobinia schizocorona (Liede & Meve) Liede & Meve, comb. nov. Basionym: *Cynanchum schizocoronum* Liede & Meve, Novon 11(2): 171, fig. 1. 2001. TYPE: Ecuador. Chimborazo: thickets, 1200–1500 m, 20 Feb. 1955, *E. Asplund 15474* (holotype, S!).

Jobinia schizocorona was described under *Cynanchum* from just two collections from Ecuador. Unfortunately, no sequenceable material of the species could be retrieved. But its habit as small twining climbers; ovate, slightly cordate leaves; absence of prophylls; and a sciadioidal inflorescence structure show that it is best treated as a member of *Jobinia*. The species is characterized by a cyathiform corona, which is folded along the upper two thirds of its length and possesses strongly lacerate margins.

10. Jobinia streptantha (Malme) Liede & Meve, comb. nov. Basionym: *Cynanchum streptanthum* Malme, Ark. Bot. 25A(7): 8–9, tab. 7. 1932. *Oxypetalum streptanthum* (Malme) Liede & G. H. Rua, Novon 7(1): 41. 1997. TYPE: Ecuador. Pichincha: Machachu, 2800 m, 12 Nov. 1920, *I. Holmgren 950* (holotype, S!).

Jobinia streptantha belongs to a small group of superficially *Cynanchum*-like plants in South America that has been moved between various genera. In the concept presented here, it is morphologically and molecularly clearly a member of *Jobinia*. The conspicuously obclavate, erect twin follicles, together with the long rostrate style head, which misled Liede and Rua (in Liede & Meve, 1997) to affine the taxon within *Oxypetalum*, fit very well into the present concept of *Jobinia*. *Jobinia streptantha* is retrieved with very good support (MP/ML: 95%/96% BS, BI: 1.00 PP) as sister of *J. tarmensis* (Fig. 1); both are fairly robust plants with coriaceous leaves bearing two conspicuously large colleters at the base of the lamina. Florally, however, the two species are quite dissimilar, except that they both possess a rostrate style head.

Cynanchum longirostrum (K. Schum.) W. D. Stevens is likewise a member of this group of species, as Stevens (1988) correctly pointed out. Because its holotype (Ecuador. Guayas: prope Naranjito, Aug. 1891, *A. Sodiro 107/3*) has been lost in B and only a photograph of the holotype could be traced in F!, the name cannot be formally transferred to *Jobinia*. However, closer inspection of the photograph revealed that the plant depicted shares with *J. streptantha* the stout stems (main stems to 4 mm diam., side branches to 2.5 mm diam.), the narrow spacing of the leaves along the side branches, shape and size of the leaves, and the almost globular, many-flowered inflorescences. Details of floral structure, however, are not visible. From the protologues, it can be gathered that the flowers of *C. longirostrum* are slightly smaller than those of *J. streptantha* (e.g., corolla lobes 5.3 mm vs. 8–9 mm long), but not fundamentally different in structure. Both species are recorded from Ecuador. It is therefore likely that *C. longirostrum* in its original circumscription is identical to or at least very closely related to *J. streptantha*.

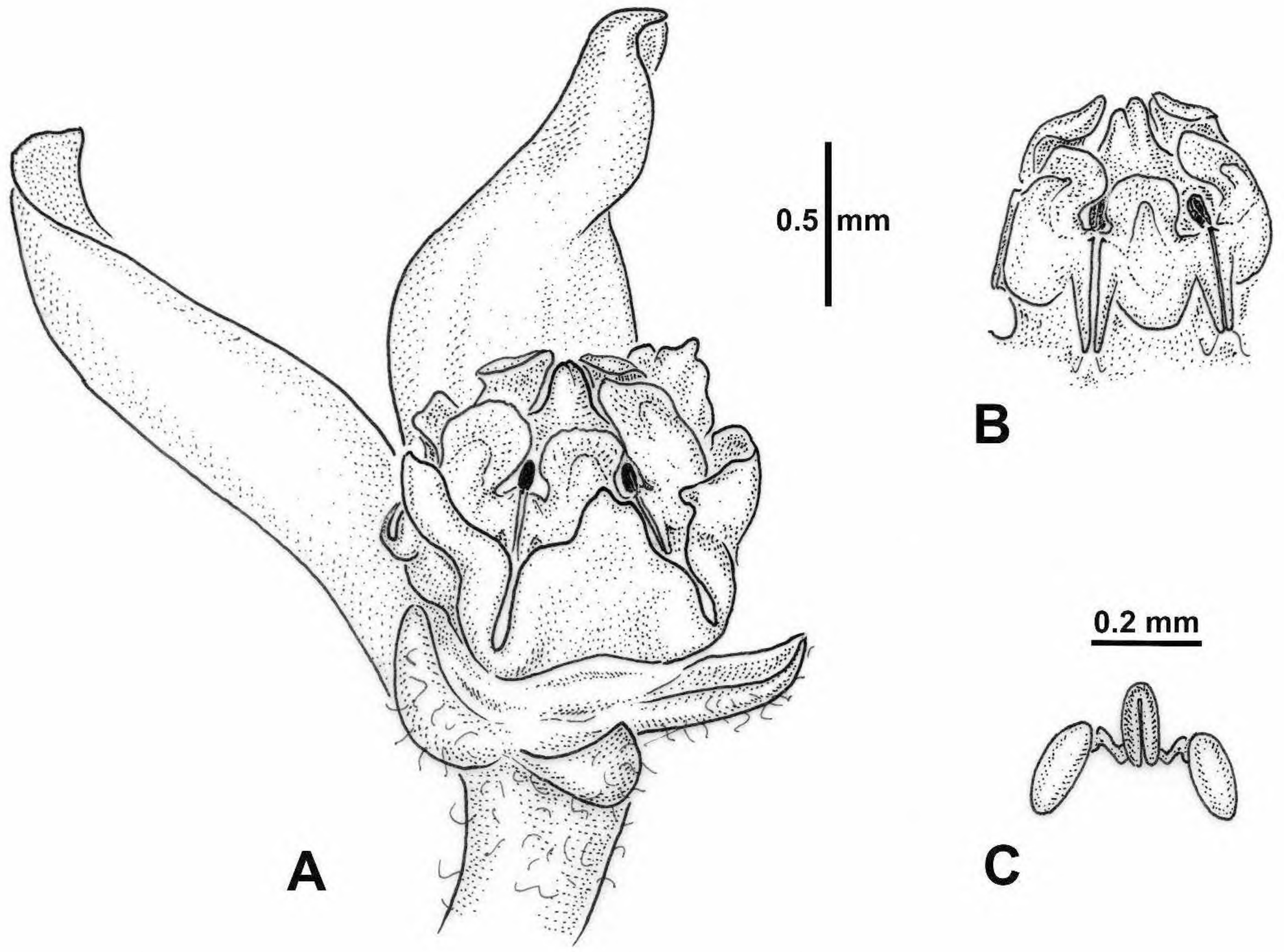


Figure 5. *Jobinia samuelssonii* (Malme) Liede & Meve. —A. Flower, lateral view. —B. Gynostegium. —C. Pollinarium. A–C from holotype *Venturi 4439* (S). Drawn by U. Meve.

Additional specimens examined. BOLIVIA. **Cochabamba:** Carrasco, ca. 0.5 km from Monte Puncu toward Sehuencas, 2900 m, *Wood 10318* (K); 2700 m, *11557* (K, UBT); Quillacollo, Chorojo, 3600 m, 28 Aug. 1990, *Hensen 887* (USZ); Arque Prov., Sihuyalla, 3300 m, 5 Jan. 1992, *Ibisch 832* (LPB). ECUADOR. **Bolívar:** above Guaranda, ca. Km. 10 to Riobamba, 01°37′S, 58°57′W, 2880 m, *Liede & Meve 3550* (UBT).

11. Jobinia tarmensis (Schltr.) Liede & Meve, comb. nov. Basionym: *Cynanchum tarmense* Schltr., Bot. Jahrb. Syst. 37: 621. 1906. TYPE: Peru. Junin Region: Tarma, *A. Weberbauer 1740* (lectotype, designated here, G!). Figure 10D.

Of the two syntypes given by Schlechter, only one, *Weberbauer 1740*, could be traced in G and is selected as the lectotype. The other syntype, *Weberbauer 1790*, was not located. *Jobinia tarmensis* is one of the two more frequent *Jobinia* species and has been recorded from Peru, in the regions of Ancash, Apurí, Cajamarca, Cuzco, Huánuco, Junín, La Libertad, and Pasco. A record from the northern Ecuadorian Province of Carchi, based on *Boom et al. 1399* (AAU!, QCNE!, US not seen) and cited by Jørgensen and Ulloa Ulloa (1994: 88) is based on a misidentification: the specimen in question represents a *Scyphostelma* and is closest to *S. pichinchensis*. A further collection from Ecuador cited by Jørgensen and Ulloa Ulloa (1994: 88), *MacBryde 357* (QCA!, US not seen), is sterile and the specimen too poor to positively identify, but leaf shape does not agree with *J. tarmensis*. Thus, there is as yet no confirmed record of *J. tarmensis* from Ecuador. *Jobinia tarmensis* is well characterized by fairly large radiate-subcampanulate flowers with broadly deltoid corolla lobes and long, spreading, ribbon-shaped, apically emarginate corona lobes (Fig. 10D; see also the discussion under *J. streptantha*).

Additional specimens examined. PERU. **Huánuco:** 2 km SW of La Union (along old rd.), 3180 m, 26 Sep. 2000, *Liede & Meve 3452* (UBT). **Lima:** rd. from Yauyos to Jauja, after Tomas, 2300 m, 7 Oct. 2002, *Weigend, Ackermann & Cano 7250* (HUSA, M, NY, SB, UBT, USM).

12. Jobinia tiarata (Malme) Liede & Meve, comb. nov. Basionym: *Cynanchum tiaratum* Malme, Ark. Bot. 25A(7): 7, tab. 5. 1932. TYPE: Peru. Arequipa: La Union, Alca near Cotahuasi, ca. 2800 m, Mar. 1914, *A. Weberbauer 6875* (lectotype, designated here, MO!; isotypes, F not seen, NY!, P!).

Jobinia tiarata, of which no material for sequencing was available, is a rare Peruvian endemic. With

its multiflorous and lax inflorescences, also found in other species of *Jobinia* (e.g., *J. balslevii*, Fig. 2A), and large (to 8 mm long) flowers with a long tubular corona, it is highly reminiscent of *J. formosa*. However, while the corona in *J. formosa* is nearly completely fused, plicate, and emarginate, the corona in *J. tiarata* is not plicate, and only fused for about half its length, and crowned (hence the name) by five long, slenderly lanceolate, free and erect lobules.

Additional specimen examined. PERU. **Arequipa:** Callo-ma, 15°39′S, 071°50′W, 3300–4000 m, 22 Apr. 2006, *H. van der Werff et al. 20923* (MO).

13. Jobinia trifurcata (Griseb.) Liede & Meve, comb. nov. Replaced synonym: *Cynanchum argentinense* Liede, in R. Govaerts, World Checkl. Seed Plants 3(1): 21. 1999. Basionym: *Metastelma trifurcatum* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 227. 1879. *Cynanchum trifurcatum* (Griseb.) Lillo, Physis 4: 423. 1919, nom. illeg,. non *Cynanchum trifurcatum* Schltr., Bull. Herb. Boissier 4: 448–449. 1896. TYPE: Argentina. Prov. Catam: Juntas, Quebrada de Choya, Nov. 1872, *F. Schickendantz 48* (lectotype, designated here, GOET!). Figure 10E.

Although the holotype specimen at B is no longer extant, a duplicate in GOET could be traced and is designated as lectotype here.

Jobinia streptantha, *J. umbellata*, and *J. trifurcata* belong to a group of species that are very difficult to separate from each other morphologically. The three species share a delicate, whitish corolla with triangular to lanceolate pointed lobes and a rostrate style head. *Jobinia streptantha* and *J. umbellata* (see also discussion under these species), however, can be separated from *J. trifurcata* s.l. by a stronger, more rigid habit, thicker stems with broadly elliptical leaves, and compact sciadioidal inflorescences. *Jobinia trifurcata* s.l. plants, in contrast, represent thin-stemmed twiners with membranous, lanceolate, and long-acuminate leaves and less compact inflorescences with longer peduncles and petioles. Plants of this stature, however, show considerable variation in flower structure, and we assume that one or two additional undescribed species are hidden in this South Andean complex. Typical *J. trifurcata* (*Liede-Schumann et al. 3636*, Fig. 10E) from Argentina has the smallest flowers, with short, triangular corolla lobes (ca. 2 mm long); an emarginate, shortly lobed corona; ovoid anthers (fertile part); bent, S-shaped caudicles; and a very short style head rostrum (not exceeding 0.5 mm in length). A plant from Bolivia sequenced here and in Liede-Schumann et al. (2005) under "*Cynanchum longirostrum*" (*Wood & Goyder 15578*) has larger flowers with longer and smaller corolla lobes (ca. 4 mm long), lingulate and notched corona lobes (free for more than 1 mm), rectangular anthers (fertile part), a considerably longer rostrum (> 2 mm long), but also bent, S-shaped caudicles. A third element (e.g., *Wood 8727*, Bolivia) is intermediate between these two with regard to the corolla, with a corona that is more deeply divided into five separated lobes but without lingulate extensions and ovoid anthers as in *J. trifurcata* s. str., and a style head rostrum of intermediate length (0.8–1 mm). In contrast to the other two elements, however, the pollinaria have straight (not bent) caudicles, and the pollinia are ovoid (instead of slenderly obovate). In our molecular study, the three accessions of this group defined by flower morphology are not monophyletic, but group according to distribution with very good support (for *J. streptantha* in sister-group position to *J. tarmensis* [MP/ML: 99%/96% BS and BI: 1.00 PP] and for the group of *J. trifurcata L 3636*, *J. umbellata*, *Jobinia* sp. *Wood 15587*, and *J. trifurcata Wood 15308* [MP/ML: 97%/99% BS and BI: 1.00 PP]). *Wood 15308* (Bolivia) and *Liede et al. 3636* (Argentina) unquestionably belong to *J. trifurcata* s. str. morphologically, even though they are not retrieved as monophyletic, whereas *Wood & Goyder 15578* (Bolivia), one of the differing and unnamed elements, is sister to *J. trifurcata* from Bolivia (*Wood 15308*).

Additional specimens examined. ARGENTINA. **Catamarca:** Comasí, La Junta, 1960 m, *Jørgensen 1162* (MO, SI). **Córdoba:** Chelecito, entre Miranda y Bordo Atravesa (Ruta 40: Km. 546), *Hunziker 22669* (CORD); Cruz del Eje, Falda E de Sierra Grande, El Mirador, antes de Cuchilla Nevada, al N de los Gigantes, *Hunziker 8794* (CORD). **La Rioja:** Capital, Mina del Cantadero, 2000 m, *Meyer s.n.* (SI); betw. Bordo Atravesa & Miranda, in a little gorge, 2000 m, *Liede-Schumann et al. 3636* (CORD). **San Juan:** Angaco, Sierra de la Pie de Palo, subiendo por el camino al Mogote Los Corralitos, en la Quebrada del Molle, *Hunziker et al. 23862* (CORD). **San Luis:** Sierra del Morro, *Pastore s.n.* (SI). BOLIVIA. **Chuquisaca:** E side of Cerro Chataquila, 3400 m, *Wood 8727* (K); Azurduy, in gorge below La Angostura, ca. 4 km below Azurduy, 2500 m, *Wood et al. 15308* (K, UBT).

14. Jobinia umbellata (Rusby) Liede & Meve, comb. nov. Basionym: *Vincetoxicum umbellatum* Rusby, Mem. Torrey Bot. Club 6: 78. 1896. Replacement name: *Cynanchum rusbyi* Malme, Ark. Bot. 25A(7): 9. 1932. Non *Cynanchum umbellatum* Vell., Fl. Flumin. 120: 3. 1825 [1829]; Fl. Flumin. Icones 3: tab. 73. 1827 [1831]. *Oxypetalum rusbyi* (Malme) Liede & Meve, Novon 11(2): 173, fig. 2. 2001. TYPE: Bolivia. Sorata, Nov. 1892, *M. Bang 1620*

(lectotype, designated here, US [barcode] 00112345!; isolectotypes, F!, GH!, MICH not seen, MO!, NY!, US [barcode] 00623894!).

Rusby (1896) wrote: "Vic. Sorata, Nov., 1892 (1620). The same as Mandon's no. (*356*?) and also collected by Pearce in Bolivia." From this statement, it becomes clear that he regarded *Bang 1620* as the type collection and the other two collections (*Mandon 356* and *Pearce s.n.*) as paratypes and did not cite all three collections as syntypes. Therefore, the lectotype has to be selected among the numerous duplicates of the *Bang 1620* collection and not, as argued in Liede and Meve (2001: 173) among the duplicates of *Mandon 356*.

Malme (1932) pointed out the similarity of *Jobinia streptantha* with *J. umbellata*. Both species share a twisted corolla and long style head, so that they were both transferred to *Oxypetalum* subg. *Cryptodus* (E. Fourn.) T. Mey. (Meyer, 1943), the only *Oxypetalum* group without translator appendages. Both species also possess a gynostegial corona of fused staminal and interstaminal lobes, but they differ in the staminal lobes exceeding the interstaminal lobes in *J. streptantha*, whereas both reach the same length in *J. umbellata*. Further, the pollinaria of *J. umbellata* are nearly twice as large as those of *J. streptantha*. Finally, the follicles differ considerably, being obclavate with a long beak in *J. streptantha* but fusiform and with a short beak at the most in *J. umbellata*. Both species are clearly placed in *Jobinia* by molecular analysis (Fig. 1), though on different subclades. This placement is better supported by leaf shape and habit than one in *Cynanchum* (lacking prophylls) or *Oxypetalum* (lacking translator appendages).

Additional specimens examined. BOLIVIA. S. loc., *Pearce s.n.* (NY). **La Paz:** Vic. Sorata, Feb. 1860, *Mandon 356* (S); Saavedra, just below bridge, ca. 11 km below Charazani on rd. to Apolo, 2700 m, *Wood 15445* (K); just above Laripata, on rd. ca. 10 km from Sorata to Mapiri, 3300 m, *Wood in Goyder 15798* (K). PERU. **Cajamarca:** Contumazá, entrada de Bosque Cachil, 2500 m, *Sagástegui et al. 15124* (F).

II. Monsanima Liede & Meve, gen. nov.

Hoc genus inter genera subtribus *Orthosiinarum* quoad laminam foliarem linearem usque lanceolatam etiam inflorescentiam plerumque foliis breviorem *Orthosiae* Decne. et *Scyphostelmati* Baill. similis, sed ab eis antherarum alis basaliter valde centrifugis per antherae longitudinem totam non productis atque corona in tubum apice inflexum gynostegium occultantem connata distinguitur.

Plants as slender twiners. Inflorescences pedunculate. Flower with a corona of highly fused staminal lobes, folded inward atop the gynostegium; gynostegium with short, strongly centrifugal anther wings; pollinaria with short, broad, horizontal translator arms. Fruits solitary, spindle-shaped.

Distribution. As far as is currently known, *Monsanima* comprises only one species, *M. morrenioides* (Goyder) Liede & Meve, a narrow endemic restricted to the Pico das Almas, Bahía, Brazil.

Monsanima morrenioides, well illustrated in the protologue of *Cynanchum morrenioides* Goyder (Goyder, 1993: fig. 1A–D), is morphologically similar to some Madagascan *Cynanchum* species, like *C. obovatum* (Decne.) Choux, with its highly fused corona that obscures the gynostegium. However, this taxon is molecularly clearly distinguished as a member of the MOOG alliance (Liede-Schumann et al., 2005). For Goyder (1993), the fruits were still unknown; however, one specimen of *M. morrenioides*, *Atkins et al. (CFCR 14739)*, revealed an apparently solitary mericarp, ca. 8 cm long, spindle-shaped, and with a long beak. This is by far the most common fruit type in the MOOG alliance; in Orthosiinae, however, it is found only in *Monsanima* and some *Scyphostelma* species, while *Jobinia* and *Orthosia* have paired fruits as a rule.

Etymology. The genus name refers to the only known locality at the Pico das Almas.

Included species. The solitary taxon in this genus is *Monsanima morrenioides* (Goyder) Liede & Meve.

1. Monsanima morrenioides (Goyder) Liede & Meve, comb. nov. Basionym: *Cynanchum morrenioides* Goyder, Kew Bull. 48: 21, fig. 1. 1993. TYPE: Brazil. Bahia: Mun. Agua Quente, Pico de los Almas, 1250 m, 16 Dec. 1988, *R. M. Harley, B. Stannard, J. R. Pirani & A. Furlan 27541* (holotype, SPF not seen; isotype, K!). Figure 10A.

Additional specimen examined. BRAZIL. **Bahia:** Rio de Contas, Estrade entre o Distr. Mato Grosso e o pé do Morro de Itabira, 1400–1600 m, 1 Mar. 1994, *S. Atkins, C. M. Sakuragui, R. M. Harley, P. T. Sano & V. C. Sousa sub CFCR 14739* (SPF).

III. Orthosia Decne., Prodr. [DC.] 8: 526. 1844. TYPE: *Orthosia congesta* (Vell.) Decne., Prodr. [DC.] 8: 527. 1844 [≡ *Cynanchum congestum* Vell.].

Since its recognition as a taxonomic unit independent of *Cynanchum* by Liede (1997), *Orthosia* has been understood as a medium-sized genus in the Orthosiinae, with approximately 31 species widely spread from southern North America to central Argentina. Its taxonomic history has been lately

summarized in Liede-Schumann and Meve (2008), and a species-level revision by the same authors is well advanced. However, the molecular results presented here (Fig. 1A) show that the present morphological circumscription of the more widespread species is often not delimiting monophyletic groups (e.g., *O. scoparia*, *O. bonplandiana*, *O. ellemannii*), requiring more detailed analyses both from the molecular and the morphological angle. The molecular results indicate clearly, though, that one taxon described by Schlechter (1916) as *O. thymifolia* Schltr., is not a member of the genus *Orthosia*, nor of the Orthosiinae, but rather belongs to the Metastelmatinae (Fig. 1B). Our one accession from Peru nests with three other taxa in *Ditassa* R. Br. and is thus affined within the Metastelmatinae. Therefore, the species is transferred to *Ditassa* here.

Included species. The 31 taxa of *Orthosia* are listed here; those included in the molecular analysis are indicated in boldface. ***Orthosia angustifolia*** (Turcz.) Liede & Meve [≡ *Metastelma angustifolium* Turcz.], ***O. bonplandiana*** (Schult.) Liede & Meve, ***O. calycina*** (Schltr.) Liede & Meve, *O. cardozoi* (Morillo) Liede & Meve, *O. cassythoides* (Suess.) Liede & Meve, ***O. congesta*** (Vell.) Decne., *O. cynanchoides* W. D. Stevens, *O. dusenii* (Malme) Fontella, *O. eichleri* E. Fourn., ***O. ellemannii*** (Morillo) Liede & Meve, *O. extra-axillaris* W. D. Stevens, *O. guilleminiana* (Decne.) Liede & Meve, *O. henriqueana* (Silveira) Liede & Meve, *O. itatiaiensis* Malme, ***O. kunthii*** Decne., *O. loandensis* Fontella & C. Valente, ***O. meridensis*** (Morillo) Liede & Meve, *O. parviflora* (E. Fourn.) Liede & Meve, ***O. pearcei*** (Rusby) Liede & Meve, ***O. pubescens*** (Greenm.) Liede & Meve, *O. ramosa* W. D. Stevens, ***O. scoparia*** (Nutt.) Liede & Meve, *O. selloana* (E. Fourn.) Liede & Meve, *O. smaragdina* W. D. Stevens, *O. stannardii* (Morillo) Liede & Meve, *O. stenophylla* Schltr., *O. stipitata* W. D. Stevens, *O. umbrosa* Decne., ***O. urceolata*** E. Fourn., ***O. virgata*** (Poir.) E. Fourn., ***O. woodii*** Meve & Liede.

1. Orthosia angustifolia (Turcz.) Liede & Meve, comb. nov. Basionym: *Metastelma angustifolium* Turcz., Bull. Soc. Imp. Naturalistes Moscou 25: 315. 1852. TYPE: Mexico. Veracruz: Mirador, 1000 m, Oct. 1838, *J. Linden 1353* (lectotype, designated by Liede & Meve [2008: 205], P!).

Orthosia angustifolia is a narrow endemic from the state of Veracruz, Mexico, where it grows in dense tangles at forest margins. It was included in the synonymy of *O. guilleminiana* by Liede and Meve (2008), but differs by more slender leaves (length: width ratio of 7.5–8.25 vs. 2.8–4) and inconspicuous, but constant, gynostegial characters. Its trapezoidal anthers are as long as the gynostegium and possess slender, nonprotruding anther wings, whereas the hemispherical anthers of *O. guilleminiana* are only half as long as the gynostegium, but display massive, protruding anther wings. Geographically, *O. angustifolia* takes an intermediate position between *O. kunthii* to the north and *O. guilleminiana* to the south. From *O. kunthii*, *O. angustifolia* differs by a corona shorter than the gynostegium, with apically truncate, vaguely trifid lobes, as opposed to a corona at least equaling the gynostegium in length, with acute to acuminate lobes.

Additional specimens examined. MEXICO. **Veracruz:** Orizaba, 8 Jan. 1867, *Botteri 2038* (P); Coatepec, 15 Aug. 1981, *Flügel & Geiseler 6023* (B); Coyame, ca. de Catemaco, 180 m, 22 Jan. 1972, *Hernandez 1384* (MEXU); 6 km en linea recta al W de San Carlos en el camino al Cerro del Diente, 1000 m, 25 Aug. 1994, *Martínez & Martínez 2457* (MEXU); 8 km NE Catemaco, 510 m, 6 Dec. 1981, *Nee 23736* (NY); Coatepec, bridge over Rio Pixquiac, 1250 m, 19 Sep. 1986, *Nee 33059* (NY, TEX); Zacuapan, Corral de las Piedras, Oct. 1906, *Purpus 2219* (NY); Xalapa, Parque "Las Tecachetes," 19 Oct. 2008, *Reyes A-5219* (MEX).

IV. Scyphostelma Baill., Hist. Pl. 10: 252. 1890. TYPE: *Scyphostelma granatensis* Baill., Hist. Pl. 252. 1890.

Cynanchum L. sect. *Microphyllum* Liede, Novon 7(2): 176. 1997. TYPE: *Cynanchum microphyllum* Kunth.

Liedea W. D. Stevens, Novon 15(4): 622. 2005. TYPE: *Liedea filisepala* (Standl.) W. D. Stevens.

The holotype of *Scyphostelma granatensis* is *Goudot s.n.* (P!) from Colombia, and the genus was monotypic until this treatment. The generitype reveals a plant with distinct long and short shoots and small, coriaceous, heart-shaped leaves, both densely covered with trichomes. The almost sessile, open-campanulate flowers bear two rows of trichomes on the adaxial side of the corolla lobes. The gynostegium is seated atop a stipe, and the prominent guide rails extend over the whole length of the anther, curving outward at the base along spreading, pointing, basal extensions of the anthers. Dorsally, the anthers are keeled, whereas the staminal corona is restricted to a short erect tooth that is confluent with the anther keel. With this character combination, although unique within Asclepiadoideae, the previously monospecific genus fits well with the concept of *Cynanchum* sect. *Microphyllum* Liede (Liede, 1997). The present paper confirms the position of members of *Cynanchum* sect. *Microphyllum* within the Orthosiinae, but outside of *Cynanchum* and Cynanchinae, respectively. It formalizes the transfer of 23 *Cynanchum* species, two *Orthosia* species (*O. ecuadorensis* Schltr., *O. trianae* Schltr.), and one *Liedea* W. D. Stevens species (*L. filisepala* (Standl.) W. D. Stevens). This paper focuses on taxa that have been used for molecular analysis

herein, or have been attributed to *Cynanchum* sect. *Microphyllum* previously (Liede, 1997; Liede & Meve, 2001), or are needed for the publication of the Catálogo de las Plantas de Colombia. Additionally, we sequenced material from six taxa that may represent undescribed taxa based on their robust affiliation within *Scyphostelma* and the Orthosiinae (Fig. 1A). *Scyphostelma* is the oldest name available for this broad assemblage of species. *Scyphostelma* presently comprises 27 species and is centered in the Andes. Numerous species so far described under "*Cynanchum*" in South America probably also belong to *Scyphostelma*, so that as many as 50 species may be expected in the genus. Flowers are mostly small (< 5 mm diam.), but highly variable in construction and coloration. Typically the corona is a bowl- to cup-shaped structure composed of five basally fused corona lobes; structural variations, such as a corona fused for more than half of its length (e.g., *S. carmenaemiliae* (Morillo) Liede & Meve), or corona lobes reduced to scales (e.g., *S. granatensis*) or corona lobes subdivided into two hardly fused lobules, resulting in a seemingly 10-partite corona (e.g., *S. bifida* (Liede & Meve) Liede & Meve) are rare. An adherence to a growth form of irregular long shoots that give rise to short shoots with very evenly distributed, distichous leaves is probably the best character to identify members of the genus, but, as is the case with all other characters checked, not all species follow this pattern (e.g., *S. harlingii*). Fruits are usually single, but occasionally also twin mericarps are formed. These, however, are fusiform and often with a fairly long beak, whereas those of *Orthosia* tend to be narrowly oblong to lineariform and with no more than a short beak. *Scyphostelma* is one of the least known genera in American Asclepiadoideae, and many species are as yet undescribed. A more detailed revision is underway by the authors.

Included species. The 27 species of *Scyphostelma* are listed here, plus six presumably new, unnamed taxa. Those included in the molecular analysis are indicated in boldface. ***Scyphostelma beckii*** (Morillo) Liede & Meve [≡ *Cynanchum beckii* Morillo], ***S. bifida*** (Liede & Meve) Liede & Meve [≡ *C. bifidum* Liede & Meve], *S. brachyphylla* (K. Schum.) Liede & Meve [≡ *C. brachyphyllum* K. Schum.], *S. carmenaemiliae* (Morillo) Liede & Meve [≡ *C. carmenaemiliae* Morillo], *S. chimboracensis* (Morillo) Liede & Meve [≡ *C. chimboracense* Morillo], *S. confusa* (R. W. Holm) Liede & Meve [≡ *C. confusum* R. W. Holm], ***S. ecuadorensis*** (Schltr.) Liede & Meve [≡ *Orthosia ecuadorensis* Schltr.], *S. filisepala* (Standl.) Liede & Meve [≡ *Metastelma filisepalum* Standl., *S. granatensis* Baill., ***S. harlingii*** (Morillo) Liede & Meve [≡ *C. harlingii* Morillo], *S. intricata* (K. Schum.) Liede & Meve [≡ *C. intricatum* K. Schum.], *S. isidrensis* (Morillo) Liede & Meve [≡ *C. isidrense* Morillo], ***S. lechleri*** (Morillo) Liede & Meve [≡ *C. lechleri* Morillo], *S. longecalicina* (Morillo) Liede & Meve [≡ *C. longecalicinum* Morillo], *S. luteynii* (Morillo) Liede & Meve [≡ *C. luteynii* Morillo], ***S. microphylla*** (Kunth) Liede & Meve [≡ *C. microphyllum* Kunth], *S. nubicola* (Morillo) Liede & Meve [≡ *C. nubicola* Morillo], *S. pichinchensis* (K. Schum.) Liede & Meve [≡ *C. pichinchense* K. Schum.], *S. ruizteranii* (Morillo) Liede & Meve [≡ *C. ruizteranii* Morillo], *S. serpyllifolia* (Kunth) Liede & Meve [≡ *C. serpyllifolium* Kunth], *S. siderocalyx* (Morillo) Liede & Meve [≡ *C. siderocalyx* Morillo], *S. sodiroi* (K. Schum.) Liede & Meve [≡ *C. sodiroi* K. Schum.], *S. tenella* (L. f.) Liede & Meve [≡ *C. tenellum* L. f.], *S. trianae* (Schltr.) Liede & Meve [≡ *O. trianae* Schltr.], *S. veleziae* (Morillo) Liede & Meve [≡ *C. veleziae* Morillo], ***S. velutina*** (Morillo) Liede & Meve [≡ *C. velutinum* Morillo], ***S. wurdackii*** (Morillo) Liede & Meve [≡ *C. wurdackii* Morillo], ***Scyophostelma* sp. indet. a, b, c, d, e, f** (all from Ecuador).

1. Scyphostelma beckii (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum beckii* Morillo, Ernstia 4(1–2): 3–4, 9. 1994. TYPE: Bolivia. La Paz: Murillo, NNE de La Paz, Valle de Zongo, bajando de la represa del lago Zongo 22.5 km, 2800 m, 2 Apr. 1988, *S. Beck 13819* (holotype, LPB!; isotype, MERF!).

With its short internodes, and thus very narrowly spaced leaves, and small, coriaceous, hirsute and heart-shaped, mucronate leaves with stout colleters at the base of the lamina, *Scyphostelma beckii* vegetatively is hardly distinguishable from species such as *S. granatensis* or *S. isidrensis* from Venezuela. Florally, *S. granatensis* is very different (see discussion above), while *S. isidrensis* and *S. beckii* can be distinguished only by details of the corona and the gynostegium (corona lobes rectangular-lingulate and sub-emarginate, and gynostegium higher than broad in *S. beckii*; corona lobes broadly obovate, trilobed, tipped by an incurved lobule, and gynostegium broader than high in *S. isidrensis*). Together with the Peruvian accession of *S. microphylla*, *S. beckii* forms one of the three unresolved, very well-supported main clades in *Scyphostelma*.

Additional specimens examined. BOLIVIA. **La Paz:** Murillo, 22 km below Zongo Dam by rd. along Zongo Valley, 3000 m, 7 May 2000, *Wood 16326* (K, UBT); Zongo-Valley, 23 km from top, 2850 m, 13 May 1993, *Liede & Conrad 3141* (MSUN, UBT, ULM).

2. Scyphostelma bifida (Liede & Meve) Liede & Meve, comb. nov. Basionym: *Cynanchum bifidum* Liede & Meve, Novon 7(1): 38–39, fig. 1. 1997. TYPE: Ecuador. Azuay: 1–2 km N of Nieves, Ceja forest, 3000–3100 m, 16 Nov. 1988, *G. Harling 25919* (holotype GB!; isotype, MO!). Figure 10F.

Scyphostelma bifida morphologically belongs to the group of species vegetatively characterized by a microphyllous growth form, and florally by a stipitate gynostegium raised from a corona staying close to the corolla. Uniquely, the corona lobes are completely divided (hence the name) so that the corona appears 10-lobed. Otherwise, this species is hardly distinguishable from *S. serpyllifolia*, where the corona lobes are only apically bifid. Molecularly, *S. bifida* belongs to the large clade of mainly Ecuadorian taxa.

Additional specimen examined. ECUADOR. **Azuay:** betw. Cajas pass "Tres Cruces" & Cuenca, 02°46′S, 79°11′W, 3580 m, 10 Nov. 2005, *Liede & Meve 3557* (UBT).

3. Scyphostelma brachyphylla (K. Schum.) Liede & Meve, comb. nov. Basionym: *Cynanchum brachyphyllum* K. Schum., Bot. Jahrb. Syst. 25(5): 726. 1898. TYPE: Ecuador. Pichincha: ad montem Pichincha, in silvis prope Tablahuasi, Sep. 1888, *Sodiro 107/12* (lectotype, designated here, P [barcode] 00644838!; isolectotype, G!).

Scyphostelma brachyphylla is vegetatively similar to *S. ecuadorensis*, included in the molecular analysis with its rather broad leaves covered by a dense, slightly yellowish indument. Florally, it is characterized by a long-stipitate gynostegium, as illustrated by Liede (1997: 177, fig. 2). The species was included in *Cynanchum* sect. *Microphyllum* by Liede (1997). As the holotype is obviously lost, the well-preserved isotype at P is selected as lectotype.

Additional specimen examined. ECUADOR. **Pichincha:** Mt. Pichincha, prope Nono, 20 May 1920, *I. Holmgren 654* (S).

4. Scyphostelma carmenaemiliae (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum carmenaemiliae* Morillo, Ernstia 2(1–2): 4. 1992. TYPE: Venezuela. Mérida: Carr. Estanques–El Molino, 17 km S de Estanques, 1650 m, 17 Mar. 1992, *G. Morillo, B. Eriksen & B. Ståhl 10800* (holotype, VEN!; isotype, MERF!).

The highly stipitate gynostegium in combination with a highly fused, membranous corona that surpasses the gynostegium led Liede and Meve (2001) to affine this species with *Cynanchum* sect. *Microphyllum*. The same characters now warrant its inclusion in *Scyphostelma* in the closer relationship of *S. bifida*, *S. brachyphylla*, *S. ruizteranii*, and *S. serpyllifolia*. *Scyphostelma carmenaemiliae* has a limited distribution in the high Andes of Venezuela, where it is found in montane forest and cloud forest.

Additional specimens examined. VENEZUELA. **Mérida:** Carr. Estanques El Molino, 17 km S de Estanquez, 3 Mar. 1992, *Morillo, Eriksen & Ståhl 10804* (MER, MERF). **Táchira:** Lobadera, Parque Cazadero, Carretera de Palo Grande a Minas de Carbón de Lobatera, 11 Dec. 1979, *Berti & Peña 569–979* (MER). **Trujillo:** Boconó, El Campamento, ca. 2000 m, 9–16 July 1998, *Stergios 17540* (PORT, UBT, US); Parque Nacional Guaramacal, sector quebrada Honda-Pele Ojo, El Santuario, 1950–2100 m, 2001, *Stergios & Carácas 18975* (PORT, UBT, US); Montañas de Misisí, carr. vieja Trujillo-Boconó, ca. 12 km by air NW of Boconó, 2000–2400 m, 6 July 1990, *Dorr, Barnett & Diaz P. 7286* (MERF).

5. Scyphostelma chimboracensis (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum chimboracense* Morillo, Ernstia 2(1–2): 5. 1992. TYPE: Ecuador. Chimborazo: rd. 4 km E of Alao, 78°27′W, 1°52′S, 3350–3500 m, May 1982, *B. Øllgaard, L. B. Holm-Nielsen, N. H. Andreasen, B. B. Larsen & L. P. Kvist 38042* (holotype, AAU not seen; isotype, MO!).

Scyphostelma chimboracensis is a smaller and almost glabrous version of *S. intricatum*, and, like the latter species, displays the typical long shoot–short shoot pattern of *Scyphostelma* and a stipitate gynostegium. It was considered a member of *Cynanchum* sect. *Microphyllum* by Liede (1997).

6. Scyphostelma confusa (R. W. Holm) Liede & Meve, comb. nov. Basionym: *Cynanchum confusum* R. W. Holm, Fieldiana 28: 505. 1953. TYPE: Venezuela. Mérida: "La Isla" above Tabay, 2285–2745 m, 18 May 1944, *Steyermark 56586* (holotype, F!; isotype, CAS!).

Liede and Meve (2001) placed this species in *Cynanchum* sect. *Microphyllum* because the character mix of adaxially pilose corolla lobes, corona lobes fused for more than one third of their length, and sessile, sciadioidal inflorescences affine it with taxa such as *Scyphostelma luteynii*. *Scyphostelma confusa* is well distinguished by its vertical, robust guide rails that are nearly double as long as the fertile part of the anthers and its narrowly ovoid pollinia that are apically attached to the caudicles.

7. Scyphostelma ecuadorensis (Schltr.) Liede & Meve, comb. nov. Basionym: *Orthosia ecuadorensis* Schltr., Bot. Jahrb. Syst. 37: 618. 1906. Replacement name: *Cynanchum densiflorum* W. D. Stevens, Phytologia 64(5): 333. 1988. Non *Cynanchum ecuadorensis* Schltr., Bot. Jahrb. Syst. 34 (Beibl. 78): 15. 1904. TYPE: Ecuador. "in fruticetis apertis prope Molleturo, in Andibus occid. Caucae" 2500–3000 m, Nov. 1890, *F. C. Lehmann 5646* (lectotype, designated

here, US [barcode] 00113249!; isolectotypes, G!, GH!, K!). Figure 6.

We regard the holotype (B) as destroyed. Of the studied isotypes of *Lehmann 5646*, the barcoded specimen in US (00113249) is the richest and best preserved and is therefore chosen as lectotype.

This species is easily recognizable by its heart-shaped, densely pilose leaves and multiflorous, subglobose inflorescences with as many as 20 to more than 50 flowers. The radiate flowers are fairly large, 6–8 mm in diameter, and densely pilose. The fleshy corona lobes are at least twice as long as the gynostegium, reaching over 2 mm. The folding of the corona lobes, with an adaxially double-keeled median region and abaxially strongly revolute margins in the basal half, is the most distinctive feature of the species (Fig. 6E). Molecularly, the species is placed in the large clade of Ecuadorian species.

Additional specimens examined. ECUADOR. **Chimborazo:** along E 60 from Riobamba to Bucay, 01°51′S, 78°53′W, 2950 m, 8 Nov. 2005, *Liede & Meve 3556* (UBT). **Loja:** 4 km W of Selva Alegre, Rd. Selva Alegre–Manú, primary montane forest, *Harling & Ståhl 26512* (GB, S).

8. Scyphostelma filisepala (Standl.) Liede & Meve, comb. nov. Basionym: *Metastelma filisepalum* Standl., Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 956. 1938. *Cynanchum filisepalum* (Standl.) L. O. Williams, Fieldiana, Bot. 32: 36. 1968. *Liedea filisepala* (Standl.) W. D. Stevens, Novon 15(4): 622–623. 2005. TYPE: Costa Rica. Alajuela: entre San Ramón y La Palma de San Ramón, 30 June 1928, *B. Brenes 6179* (holotype, F not seen; isotype, NY!).

Scyphostelma filisepala is a highly unusual species in its floral structure, in which the long sepal lobes by far exceed the corolla, corona, and gynostegium. Liede (1997) placed this species in *Cynanchum* sect. *Microphyllum*, but Stevens (2005) argued that the long-pedunculate, sciadioidal inflorescences, the uniformly pubescent stems, and the high-climbing habit do not fit to the remainder of species attributed to *Cynanchum* sect. *Microphyllum*. However, long-pedunculate, sciadioidal inflorescences, while rare in *Scyphostelma*, have also been found in *S. harlingii*. Uniformly pubescent stems and high-climbing habit are found in several other species of *Scyphostelma* as well, e.g., *S. ecuadorensis*. Its growth form of densely leafy, distichous floriferous short shoots and long shoots with larger leaves, which are shed with age, make it a typical member of *Scyphostelma*, and the basally fused corona and general gynostegium structure support this conclusion. *Scyphostelma filisepala* is the only known species of *Scyphostelma* in Central America and probably has undergone a long period of isolation. Unfortunately, several attempts to obtain sequenceable material of this interesting species have failed.

Additional specimens examined. COSTA RICA. **Alajuela:** Cantón de San Ramón, Cordillera de Tilarán, Zapotal, Río Barranquilla, 1500 m, 7 Sep. 1993, *Bello & Cruz 5306* (MO). **Puntarenas:** Monteverde Cloud Reserve, Pacific slope, 1500 m, 23 Oct. 1986, *Haber & Bello 6042* (MO). PANAMA. **Chiriqui:** near Costa Rican border, 13 km by rd. S of Río Sereno, Finca Hartmann, 1400–1800 m, 12 May 1991, *Hensold 1018* (MO, NY).

9. Scyphostelma harlingii (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum harlingii* Morillo, Ernstia 2(3–4): 62–63. 1992. *Blepharodon harlingii* (Morillo) Liede & Meve, Novon 11(2): 173. 2001. TYPE: Ecuador. Zamora-Chinchipe: above Valladolid, on rd. to Yangana, mtn. rainforest, 2300 m, Feb. 1985, *G. Harling & B. L. Andersson 21422* (holotype, GB!).

Scyphostelma harlingii is a very distinctive *Scyphostelma* species, lacking the characteristic long and short shoots seen elsewhere in the genus. It displays large reddish flowers (more than 1 cm diam.) in a horizontal position borne on long pedicels (ca. 2 cm) and even longer peduncles (2–4 cm). Its corolla lobes are spreading to reflexed, membranous, and glabrous. Its staminal corona lobes are almost unfused and cut to spreading fringes. The single mericarps are fairly long (8–10 cm) and laxly pendent. With this character combination, the taxon was transferred to *Blepharodon* in an earlier study (Liede & Meve, 2001). Molecular analysis, however, places our Ecuadorian accession clearly into the *Scyphostelma* clade, where it stands isolated with an accession from Bolivia (*Wood 10297*), which might constitute a new species. *Scyphostelma harlingii* is typically confined to humid quebradas (ravines).

Additional specimens examined. ECUADOR. **Zamora-Chinchipe:** Est. Cient. San Francisco, Quebrada Milagro, *Liede & Meve 3460* (UBT); *Wolff 167* (UBT); 2300 m, *Wolff 57* (UBT); along T4, *Matezki & Homeier 174* (UBT). PERU. **Húanuco:** Húanuco, Carpish, *Ferreyra 16159* (USM).

10. Scyphostelma intricata (K. Schum.) Liede & Meve, comb. nov. Basionym: *Cynanchum intricatum* K. Schum., Bot. Jahrb. 25: 727. 1898. TYPE: Ecuador. Pichincha: prope Jiatillo, Sep. 1888 (fl.), *A. Sodiro 107/11* (lectotype, designated here, fragm. at F!).

With the holotype destroyed in B, the fragment housed in F is the only piece of original material

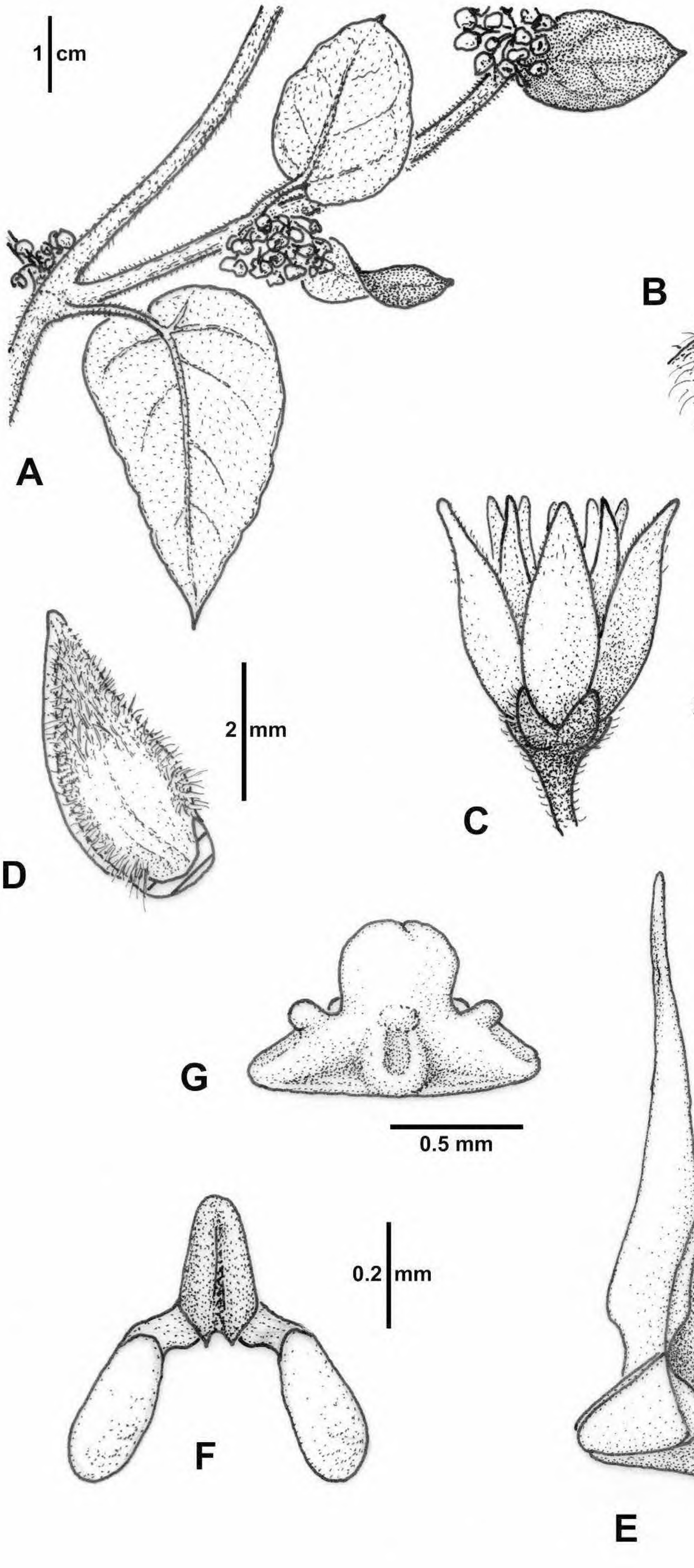


Figure 6. *Scyphostelma ecuadorensis* (Schltr.) Liede & Meve. —A. Branch with inflorescence. —B. Inflorescence. —C. Flower. —D. Corolla lobe, adaxial view. —E. Gynostegium. —F. Pollinarium. —G. Style head. A–G from isotype *Lehmann 5646* (US). Drawn by J. Conrad.

traced. However, as this fragment bears several flowers, it is chosen as lectotype here.

Scyphostelma intricata was listed among the members of *Cynanchum* sect. *Microphyllum* by Liede (1997). It is a typical *Scyphostelma* in habit, characterized by flowers with a highly stipitate gynostegium and five elongate, apically bipartite corona lobes. Its mericarps are at least occasionally paired, but their fusiform shape and long beak attribute them to *Scyphostelma*. *Scyphostelma intricata* is closely related to *S. brachyphylla*, *S. chimboracensis*, and *S. serpyllifolia*, but a more detailed study is necessary to disentangle this difficult species complex.

11. Scyphostelma isidrensis (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum isidrense* Morillo, Ernstia 2(1–2): 7, 14, fig. 1. 1992, as "*isidrensis*." TYPE: Venezuela. Mérida: betw. El Molino & ridge before descending to San Sidro Altro, alt. 2430–2895 m, *J. A. Steyermark 56256* (holotype, F not seen).

Scyphostelma isidrensis is vegetatively very similar to *S. beckii* from Bolivia, but differs in details of corona and gynostegium structure (see discussion under *S. beckii*). The protologue is accompanied by a full illustration.

Additional specimen examined. VENEZUELA. **Mérida:** 48 km from Estanquez, 6 Oct. 1998, *Liede & Meve 3320* (UTB).

12. Scyphostelma lechleri (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum lechleri* Morillo, Pittiera 23: 43. 1995. TYPE: Peru. Tabina, July 1854, *W. Lechler 2079* (holotype, P!; isotypes, K not seen, NY!, UPS!). Figure 7.

Ditassa subtrivialis Griseb., a nomen nudum (Lechler 1857: 58) is based on the same type. The locality of Tabina is not listed in modern gazettes; however, the name was a locality at Lechler's time, as the names *Andropogon tabina* Steud. (Poaceae), *Carex tabina* Steud., and *Cyperus tabina* Steud. (Cyperaceae) were all based on Lechler specimens. The Geranium Taxonomic Information System (Aedo, 2010) gives Tabina as a locality in Puno at 14°8′S, 69°32′W.

Scyphostelma lechleri displays the typical long shoot–short shoot construction of *Scyphostelma*. Its pilose adaxial corolla lobes and the short corona fused for around one third its length characterize the species in the genus. There is much resemblance with *S. confusa* from Venezuela with regard to corolla and corona (see also under *S. confusa*). However, notched corona lobes, a knobby style head, and very acute and rather erect anther appendages (Fig. 7) might be sufficient alone for delimitation of *S. lechleri*. Our Bolivian accession is included with strong support (MP/ML: 87%/84% BS, BI: 1.00 PP) in the large subclade comprising otherwise exclusively Ecuadorian accessions.

Additional specimen examined. BOLIVIA. **La Paz:** Sorata, 13 km from town on rd. to Batallas, 15°49′S, 66°58′W, 3180 m, 8 Mar. 1993, *Liede & Conrad 3136* (MSUN, ULM).

13. Scyphostelma longecalicina (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum longecalicinum* Morillo, Ernstia 2(3–4): 63–64. 1992. TYPE: Ecuador. Pichincha: Faldas occidentales del Volcán Atacazo, vegetación de Páramo secundaria y manchas de bosque con dominancia de *Polylepis sericea*, 3700–3800 m, 25 Nov. 1985, *B. B. Larsen 304* (holotype, GB not seen; isotypes, NY!, QCA not seen). Figure 8.

Scyphostelma longecalicina was included in *Cynanchum* sect. *Microphyllum* by Liede (1997) because of its characteristic habit and its clavate, long-beaked fruits unknown to Morillo (1992), which stand in an acute angle when paired. It differs from the other *Scyphostelma* species by rather large flowers (6–7 mm diam.) whose calyx lobes exceed the corolla tube considerably (Fig. 8).

14. Scyphostelma luteynii (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum luteynii* Morillo, Ernstia 2(3–4): 64. 1992. TYPE: Peru. Cuzco: Paucartambo, Paucartambo–Patria rd., 17–18 km NE of Paucartambo, along roadside slopes, alt. 3170 m, 9 Dec. 1978, *J. Luteyn & M. Lebrón-Luteyn 6436* (holotype, NY!; isotypes, AAU not seen, MO!).

Scyphostelma luteynii was included in *Cynanchum* sect. *Microphyllum* by Liede (1997) because of its characteristic habit and its clavate, long-beaked fruits, which stand in an acute angle when paired. It differs from the other *Scyphostelma* species by marginally and adaxially apically pilose corolla lobes, and a corona fused to about one third of its length combined with a stipitate gynostegium.

15. Scyphostelma microphylla (Kunth) Liede & Meve, comb. nov. Basionym: *Cynanchum microphyllum* Kunth, Nov. Gen. Sp. [HBK] (quarto ed.) 3: 204, tab. 236. 1818 [1819]. *Vincetoxicum microphyllum* (Kunth) Decne., Prodr. [DC.] 8: 525. 1844. TYPE: Ecuador. Prope Pasto, Nov., *A. Bonpland s.n.* (holotype, P!).

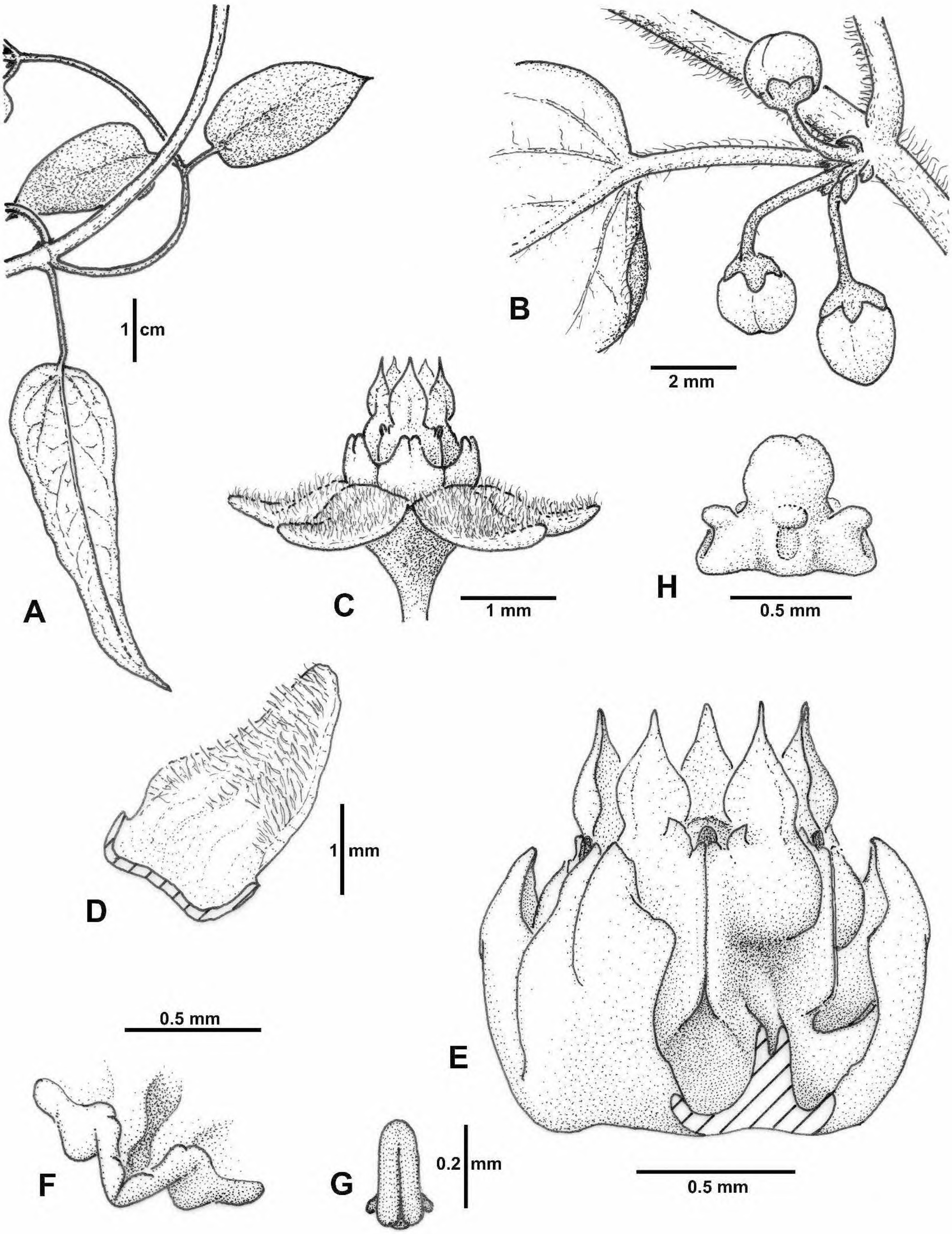


Figure 7. *Scyphostelma lechleri* (Morillo) Liede & Meve. —A. Branch with leaves. —B. Inflorescence. —C. Flower. —D. Corolla lobe. —E. Gynostegium with corona. —F. Basal guide rail opening. —G. Corpusculum. —H. Style head. A–H from isotype *Lechler 2079* (UPS). Drawn by J. Conrad.

Not immediately distinguishable from each other, *Scyphostelma microphylla* and *S. serpyllifolia* are among the most widespread and frequent *Scyphostelma* species in Ecuador, extending into Bolivia and Colombia. They represent well the concept of the genus with their almost leafless long shoots and distichous short shoots, which are often augmented by short shoots produced from adventitious buds. Their

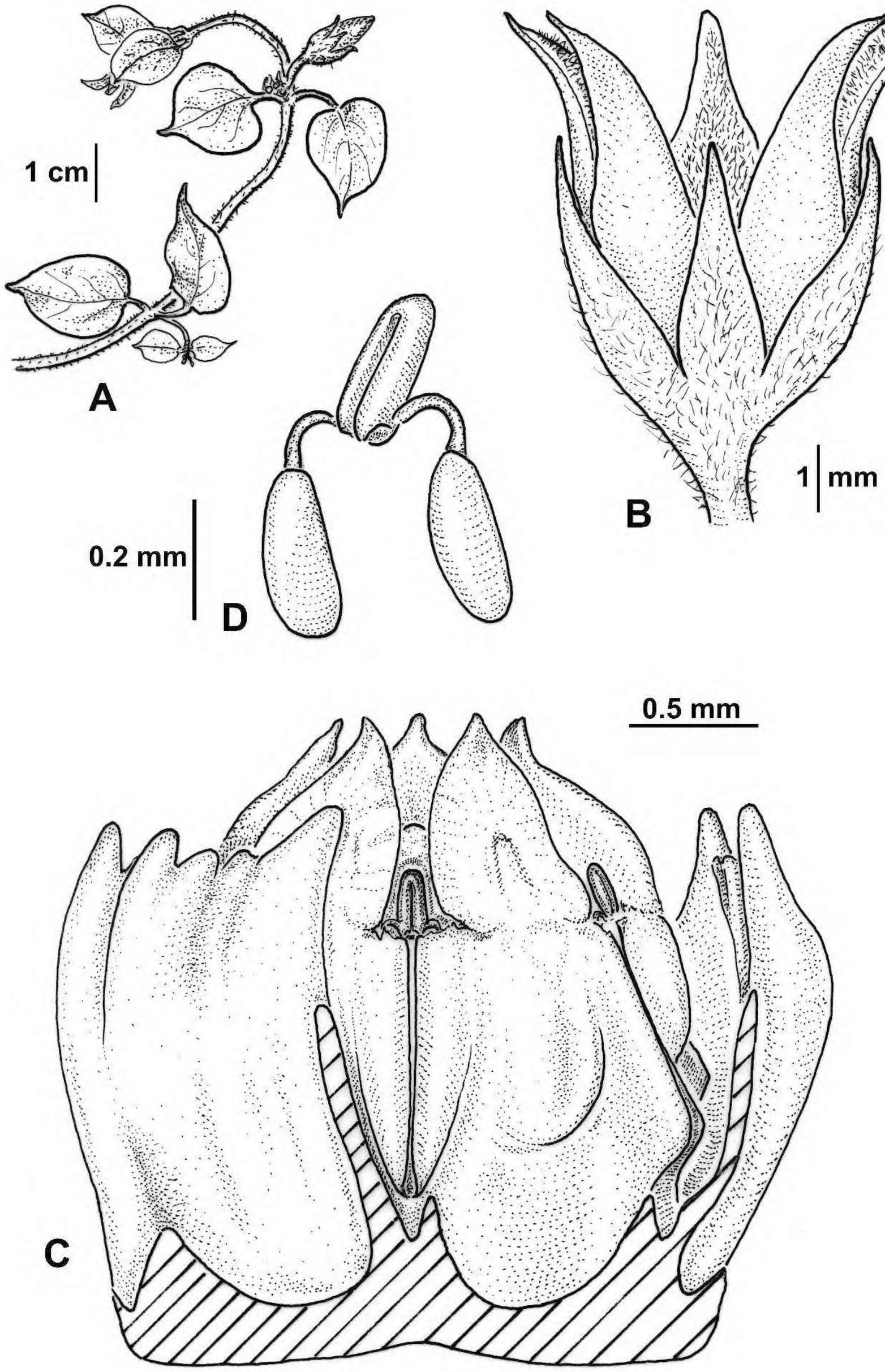


Figure 8. *Scyphostelma longecalicina* (Morillo) Liede & Meve. —A. Branch with leaves and flower bud. —B. Flower, lateral view. —C. Gynostegium with corona. —D. Pollinarium. A–D from isotype *Larsen 304* (NY). Drawn by J. Conrad, executed in ink by U. Meve.

flowers, also superficially very similar, can be distinguished based on gynostegium shape. The (sub-)sessile, broadly cylindrical gynostegium distinguishes *S. microphylla* easily from *S. serpyllifolia*, with its inversely pistilliform, stipitate gynostegium. Corona morphology seems to be fairly variable in *S. microphylla*, with entire or bifid corona lobes, and it is yet unclear how many discrete units might be distinguished in this complex. The single accession included in the molecular analysis (Ecuador, *Céron & Alcarón 12217*) is part of this complex, even though it differs from the type by adaxially pilose corolla lobes. It is a member of the well-supported clade (MP/ML: 87%/84% BS, BI: 1.00 PP) comprising predominantly Ecuadorian taxa. The taxon was illustrated in Humboldt and Bonpland (1818: tab. 236).

In the molecular analysis, a second accession originally identified by us as *Scyphostelma micro-*

phylla (*Weigend 5821*) from Peru was included. However, in contrast to the Ecuadorian accession (*Cerón & Alcarón 12217*), which is consistently a member of the large Ecuadorian clade, the former showed a very well-supported sister-group relationship to *S. beckii* from Bolivia. Upon re-inspection, it was found to differ in some aspects that had been considered minor at first, namely, a much denser indument on all vegetative parts, a dense pilose indument on the abaxial side of the corolla lobes and a scattered one on the adaxial side, and an unusually short (only ca. half of gynostegium length) corona. Together with the molecular differences, it seems best at present to treat this accession as representing a probably undescribed species (*Scyphostelma* sp. indet. f).

16. Scyphostelma nubicola (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum nubicola* Morillo, Ernstia 2: 8. 1992. *Metastelma nubicola* (Morillo) Liede, Novon 7: 43. 1997. TYPE: Venezuela. Trujillo: carr. Carrache–La Peha, 31.5 km E de Carache, 2000–2200 m, 28 Sep. 1988, *G. Morillo 10543* (holotype, VEN not seen; isotype, MERF not seen).

Scyphostelma nubicola is among the most easily distinguished microphyllous *Scyphostelma* species. Like *S. carmenaemiliae*, it possesses a long-stipitate gynostegium and baggy, rather spreading anther sacks. In contrast to *S. carmenaemiliae*, however, the corona consists of five barely fused lobes shorter than the stipe, and the whole structure is wrapped in a highly fused, ovoid-urceolate corolla. It was considered a member of *Cynanchum* sect. *Microphyllum* by Liede and Meve (2001), and is now transferred to *Scyphostelma*, where it joins the species swarm of the Venezuelan high Andes.

Additional specimens examined. VENEZUELA. **Trujillo:** Boconó. Montañas de Misisí, carr. vieja Trujillo–Boconó, ca. 12 km by air NW of Boconó, 2000–2400 m, 4 July 1990, *Dorr, Barnett & Díaz P. 7245* (MER, NY, VEN); 30 Oct. 1990, *Dorr & Barnett 7522* (NY).

17. Scyphostelma pichinchensis (K. Schum.) Liede & Meve, comb. nov. Basionym: *Cynanchum pichinchense* K. Schum., Bot. Jahrb. Syst. 25: 727–728. 1898. TYPE: Ecuador. Pichincha: "ad montem Pichincha in declivibus occidentalibus prope Palmira," Aug. 1873, *L. Sodiro 107/8* (lectotype, designated here, P!; isolectotype, G!).

The holotype at B was destroyed (photograph at F!), and of the duplicates available, the well-preserved specimen of P was chosen to serve as lectotype.

Although the leaves of *Scyphostelma pichinchensis* can grow rather large for the genus, up to 7 cm, the basally fused corona, which at least equals the gynostegium in length, and the characteristic construction of long and short shoots fit the genus well. The gynostegium is sessile with guide rails that at least double the lengths of the anthers. *Scyphostelma pichinchensis* is one of the more frequent members of the genus and is apparently widespread from Colombia to Bolivia.

Additional specimens examined. BOLIVIA. **Cochabamba:** ca. 3 km from Monte Puncu toward Sehuencas, 29 Dec. 1995, *Wood 10313* (K). COLOMBIA. **Santander:** Pamplona a Ducaramanga, páramo de Berlín, 30 May 1969, *Jaramillo 20005* (COL, GH, MA). ECUADOR. **Carchi:** ca. 50 km W Tulcán, 1 Oct. 2002, *Liede & Meve 3484* (UTB). PERU. **Ancash:** Huascarán National Park, Quebrada Ranincuray, 9°00′S, 77°33′W, 11 Jan. 1985, *Smith, Sanchez & Vidaurre 9036* (F, USZ).

18. Scyphostelma ruizteranii (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum ruizteranii* Morillo, Acta Bot. Venez. 16: 66. 1993. TYPE: Venezuela. Mérida: Rivas Dávila, Páramo Batallón, entre Portachuelo y Qda. La Mogral, 2850–2900 m, 7 May 1977, *L. Ruiz-Terán & A. Usubillaga 13501* (holotype, MERF!).

Scyphostelma ruizteranii, recognized by Liede and Meve (2001) as a member of *Cynanchum* sect. *Microphyllum*, belongs to the high Andean Venezuelan *Scyphostelma* alliance. Its stipitate gynostegium and baggy anthers affine it to *S. carmenaemiliae* and *S. nubicola*, but both the corona and the corolla are only basally fused. The species is known only from the type.

19. Scyphostelma serpyllifolia (Kunth) Liede & Meve, comb. nov. Basionym: *Cynanchum serpyllifolium* Kunth, Nov. Gen. Sp. [HBK] (quarto ed.) 3: 205. 1818 [1819]. *Orthosia serpyllifolia* (Kunth) Decne., Prod. [DC.] 8: 527. 1844. *Vincetoxicum serpyllifolium* (Kunth) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Ecuador. "crescit in umbrosis juxta Quito et in declivitate montis Pichinchensis, alt. 1600 m," *Humboldt & Bonpland s.n* (holotype, P!; photo ex P at F!).

Scyphostelma serpyllifolia has been confused often with *S. microphylla* because of far-reaching overall similarity in habit, inflorescence, and general floral appearance. However, the corona and gynostegium are distinctly different (see discussion under *S. microphylla*). As in other taxa of the microphyllous group of *Scyphostelma*, two flower color forms occur in *S. microphylla* and *S. serpyllifolia*, with the types

representing the light-colored (whitish or yellowish) form, in contrast to the almost equally frequent purplish forms. Further, *S. serpyllifolia* shows a wide degree of variability considering indument density on the vegetative parts. For example, we observed glabrescent to densely pubescent plants within a single population (*Liede & Meve 3482*).

Additional specimens examined. ECUADOR. **Bolivar:** above Guaranda (ca. Km. 15 to Riobamba), 3450 m, 7 Nov. 2005, *Liede & Meve 3553* (UBT). **Carchi:** El Angel, along rd. to the private Reserva "Colorado," 3380 m, 30 Sep. 2002, *Liede & Meve 3482* (UTB).

20. Scyphostelma siderocalyx (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum siderocalyx* Morillo, Acta Bot. Venez. 16: 68. 1993. TYPE: Venezuela. Mérida: Miranda, entre Las Palmas y Las Gonzales, Páramo de Palmira, 3200–3300 m, 23 May 1975, *L. Ruiz-Terán & M. Dugarte 12226* (holotype, MERF!).

Scyphostelma siderocalyx has been recognized as a member of *Cynanchum* sect. *Microphyllum* by Liede and Meve (2001). With its highly stipitate gynostegium bearing baggy anthers, it belongs to the Venezuelan high Andean species swarm, next to *S. ruizterranii*, from which it is distinct only by the rusty indument on bracts, calyx, and pedicel, and the narrower and acuminate corona lobes. This species is known only from the type collection.

21. Scyphostelma sodiroi (K. Schum.) Liede & Meve, comb. nov. Basionym: *Cynanchum sodiroi* K. Schum., Bot. Jahrb. Syst. 25: 728. 1898. TYPE: Colombia. Cauca: entre Popayán y Puracé, junto al puente de Uarló, alt. 2600 m, 10 July 1939, *E. Pérez A. & J. Cuatrecasas 5890* (neotype, designated here, COL!).

The holotype of this species, *L. Sodiro 107/10*, was destroyed in B, and the photos of the type specimen that are preserved in F and G cannot serve as a formal type. The holotype originated from Ecuador: Pichincha, in "locis silvaticis prope Niebly." No further specimen of the type collection could be traced, and no new material has been collected in Ecuador. Therefore, a specimen from Cauca (Colombia), which fits the description by Schumann (1898) very well and has been identified as "*Cynanchum sodiroi*" by Woodson (following label information), is selected as neotype.

Of the *Scyphostelma* species found in Pichincha, *S. sodiroi* is characterized by corona lobes that are twice as long as the sessile gynostegium, an unusual feature in *Scyphostelma*. Vegetatively, the species resembles the much more widespread *S. pichinchensis*, a species in which corona lobes only just exceed the gynostegium.

22. Scyphostelma tenella (L. f.) Liede & Meve, comb. nov. Basionym: *Cynanchum tenellum* L. f., Suppl. Pl. 168. 1781. TYPE: Colombia. *J. Mutis 4088* (holotype, MA!; isotypes, NY!, P!, US!).

For discussion of *Scyphostelma tenella*, see *S. trianae* (below).

23. Scyphostelma trianae (Schltr.) Liede & Meve, comb. nov. Basionym: *Orthosia trianae* Schltr., Bot. Jahrb. Syst. 37: 621. 1906. TYPE: Colombia. Bogotá: Caqueza, 1700 m, *J. Triana 1933* (neotype, designated here, P [barcode] 00106972!).

Of *Scyphostelma trianae*, no type material (*J. Triana 1832*, B, NY) could be traced, except for the type photograph at NY, but the excellent description by Schlechter (1906) allows its identification in Colombian material. The sheet selected as neotype was collected by Triana himself close to Bogotá and bears numerous flowers.

On first sight, *Scyphostelma trianae* closely resembles *S. tenella*, also from Colombia, with distinct long and short shoots and sessile sciadioidal inflorescences. The flowers of both species are delicate, ca. 3 mm long and slender, with oblong and adaxially pilose, membranous corolla lobes. The corona lobes shortly exceed the elongated gynostegium that has stout, vertical guide rails, which are double as long as the anthers. However, while *S. tenella* is strictly unifariously pubescent, *S. trianae* possesses scattered trichomes in addition to the uni- to bifarious pubescence on stems and leaves. Pedicels and sepals are glabrous in *S. tenella*, but pubescent in *S. trianae*, and the pedicels of *S. trianae* are distinctly filiform and 6–10 mm long, whereas those of *S. tenella* are equally thin, but much shorter (to 4 mm). Corona lobes are smooth in *S. tenella*, but show two longitudinal adaxial keels in *S. trianae*. Most significant, the gynostegium, while completely sessile in *S. tenella*, is shortly stipitate (stipe 0.2–0.3 mm long) in *S. trianae*.

Additional specimens examined. COLOMBIA. **Bogotá:** Cordillera de Bogotá, 2800 m, *Triana 1922* (P). **Boyaca:** Arcabuco. Alto del Sote, ca. 2900–3100 m, 25 Dec. 1994, *Gonzáles 3238* (NY).

24. Scyphostelma veleziae (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum veleziae* Morillo. TYPE: Colombia. Depto. del Quindio, Mun. de Genova, camino a finca Servia–Valle

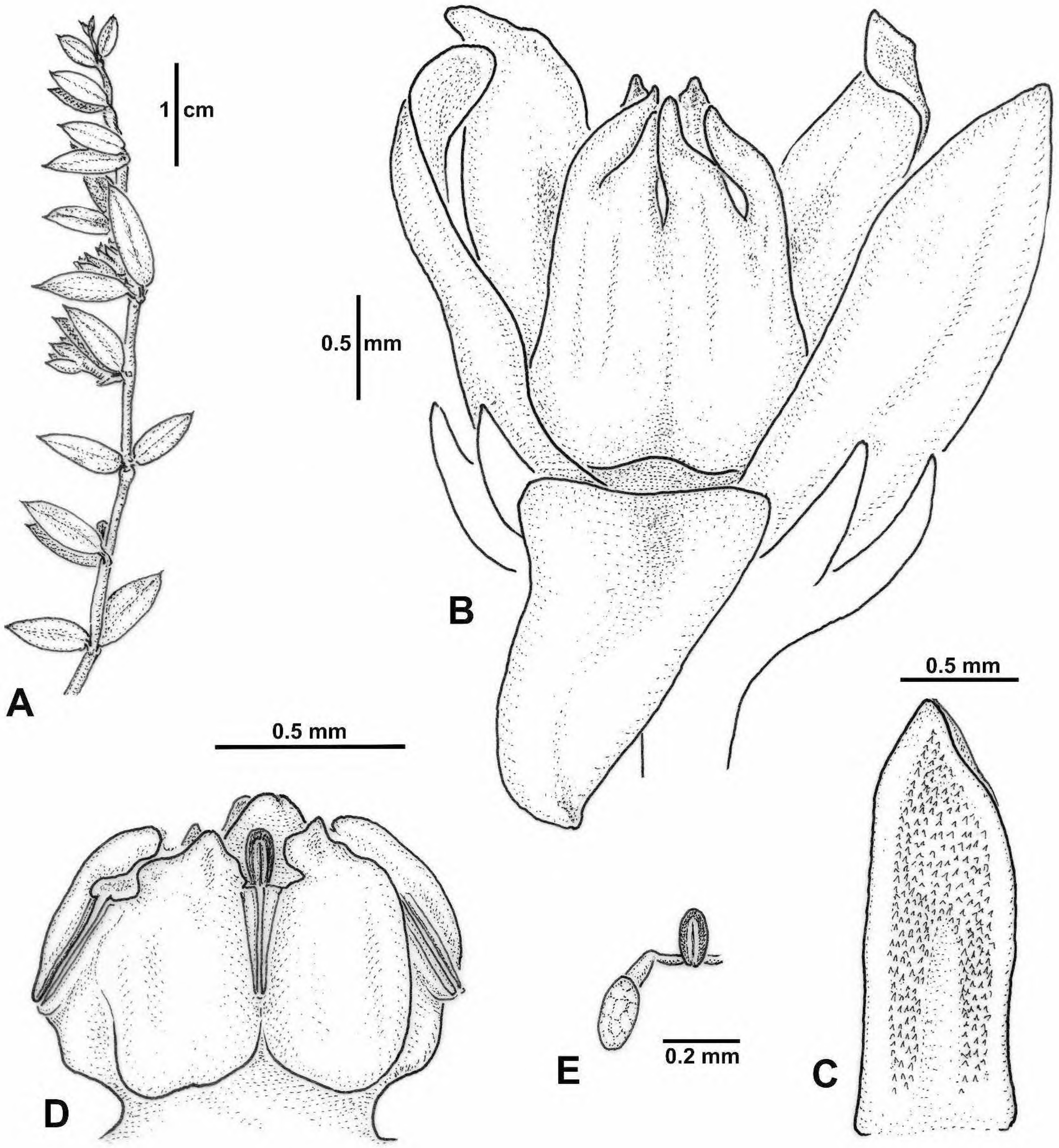
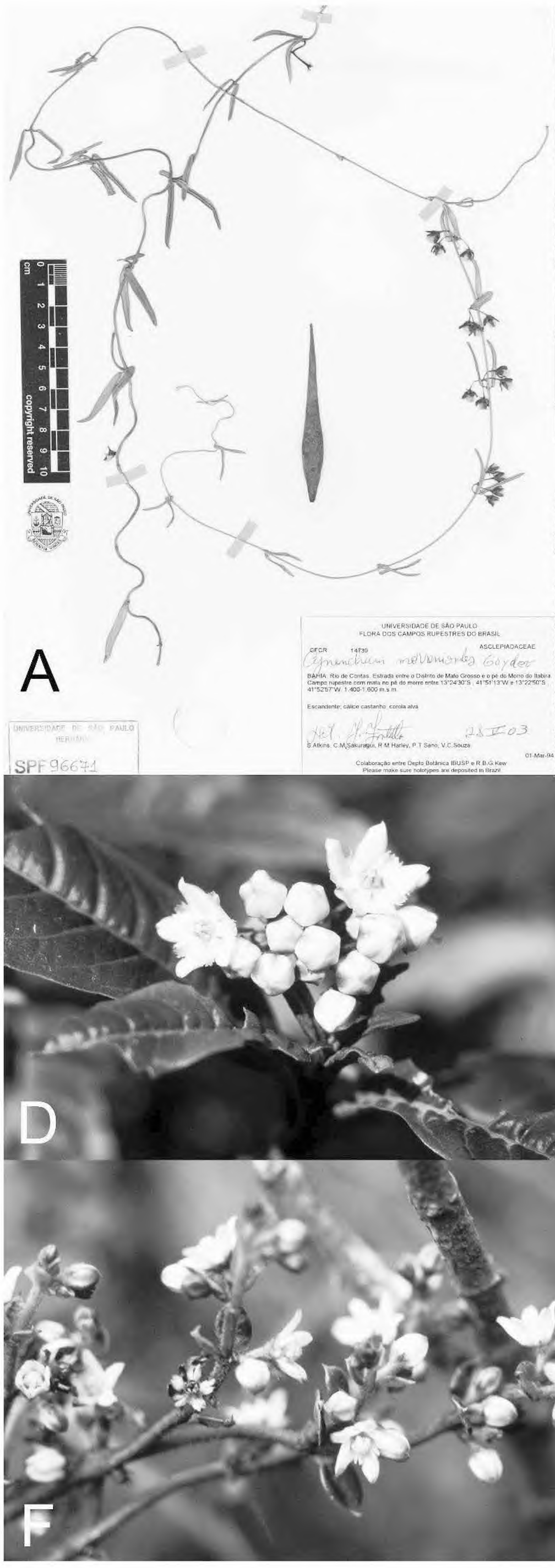


Figure 9. *Ditassa thymifolia* (Schltr.) Liede & Meve. —A. Flowering branch. —B. Flower. —C. Corolla lobe, adaxial view. —D. Gynostegium. —E. Pollinarium with one pollinium removed. A–E from lectotype *Weberbauer 6277* (US). Drawn by U. Meve.

Chiquitoen borde del bosque ante de llegar al subpáramo, 3000 m, 16 July 1990, *M. C. Vélez, C. A. Agudelo, L. F. Hoyos, V. M. Agudelo & N. J. Ocampo 2027* (holotype, HUQ not seen; isotypes, COL!, VEN!).

Scyphostelma veleziae is known only from the type collection in Colombia. It differs from its possible sister species in Ecuador, *S. brachyphylla*, by its dense indument on all vegetative parts in combination with corona lobes shorter than the gynostegium. From the Colombian endemic species pair *S. trianae* and *S. tenella*, *S. veleziae* differs by its glabrous, ovate-elliptical and rather stout corolla lobes of just 2 mm length and a distinctly stipitate (1 mm) gynostegium.

25. Scyphostelma velutina (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum velutinum* Morillo, Ernstia 2(3–4): 65. 1992. TYPE: Ecuador: Chimborazo: Pangor, Andes, Oct.



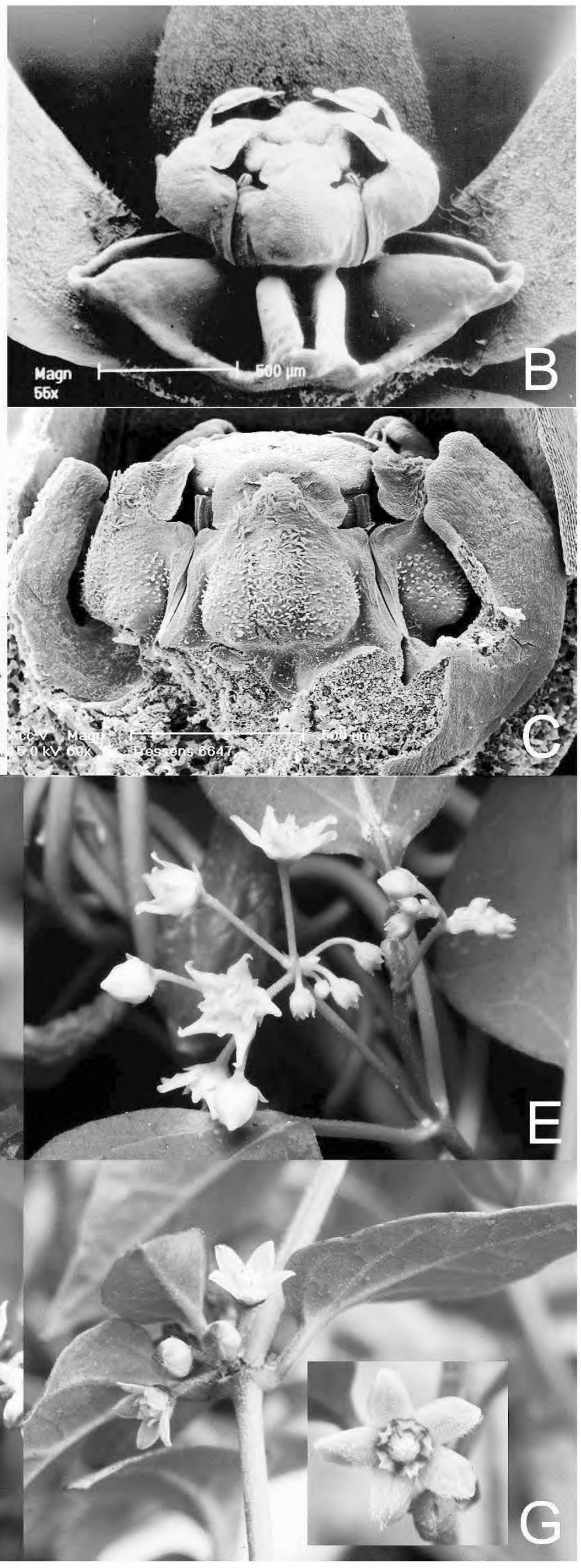


Figure 10. Representative examples for the Orthosiinae genera *Monsanima*, *Jobinia*, and *Scyphostelma*. —A. *Monsanima morrenioides*, specimen of *Atkins et al. sub CFCR 14739* (SPF). —B. *Jobinia chlorantha*, gynostegium with corona (SEM, from *Matezki 169*, UBT). —C. *Jobinia latipes*, corona (opened) showing gynostegium and shortly pilose anthers (SEM, from *Tressens et al. 6647*, UBT). —D. *Jobinia tarmensis*, flowering stem, from *Liede & Meve 3452* (UBT). —E. *Jobinia trifurcata*, flowering stem, from *Liede-Schumann et al. 3636* (CORD). —F. *Scyphostelma bifida*, flowering stem, from *Liede-Schumann & Meve 3557* (UBT). —G. *Scyphostelma pichinchensis*, from *Liede & Meve 3484* (UBT). All photographs by U. Meve.

1858, *R. Spruce 5578* (holotype, K!; isotype, BM!).

Scyphostelma velutina was included in *Cynanchum* sect. *Microphyllum* by Liede (1997) because of its characteristic habit. It belongs to the group of species with a dense yellowish indument on all vegetative parts and pilose exterior of corolla lobes. Not surprising, *S. wurdackii* is retrieved as sister species of *S. velutina* (Fig. 1) with very strong support in the molecular analysis. Both species are almost indistinguishable florally, but are easily separated by habit. *Scyphostelma velutina* branches scarcely and bears ovate(-elliptical) leaves covered by a regular velvety indument, with three to four lateral nerves protruding abaxially. *Scyphostelma wurdackii*, in contrast, develops numerous rather stiff, short shoots and bears small elliptical leaves that are discolorous due to the very dense tomentose indument on the abaxial side of the leaf that obscures the less prominent five to six lateral nerves.

Liede-Schumann and Meve re-collected this Ecuadorian endemic for the first time 147 years after the original collection of Spruce in 1858.

Additional specimen examined. ECUADOR. **Chimborazo:** along E 60 from Riobamba to Bucay, 3050 m, 8 Nov. 2005, *Liede & Meve 3555* (UBT).

26. Scyphostelma wurdackii (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum wurdackii* Morillo, Ernstia 2(1–2): 11–12. 1992. TYPE: Peru. Amazonas: Chachapoyas, moist ravine head, on middle E Calla–Calla slopes, 3–5 km SE of Km. 422, Leimebamba–Balsas rd., 3000–3200 m, 22 Aug. 1962, *J. J. Wurdack 1768* (holotype, K not seen; isotypes, G!, NY!, US!, USM!).

Scyphostelma wurdacki is one of the most characteristic *Scyphostelma* species, with its ovate, apically slightly mucronate leaves and its dense yellowish indument on the stems and lower leaf surfaces, resulting in a strong contrast between the dark green upper and the cream-colored lower leaf surfaces (see also remarks under *S. velutina*).

Additional specimen examined. ECUADOR. **Cuenca:** Parque Luis Fernando Carrion, 02°50′S, 79°09′W, 3200 m, 25 Oct. 1998, *Liede 3342* (UBT).

METASTELMATINAE

I. Ditassa R. Br., Asclepiadeae 38. 1810. TYPE: *Ditassa banksii* R. Br. ex Schult., Syst. Veg. 6: 112. 1820.

Ditassa is a large genus of Metastelmatinae in South America, comprising ca. 100 species, with about half of them from Brazil (Konno, pers. comm.). Based on molecular results, *Minaria* T. U. P. Konno & Rapini has been split from *Ditassa* recently (Konno et al., 2006). *Ditassa* is typically furnished with a gynostegial corona of free, rarely basally fused, staminal lobes, differentiated into a proximal and a distal lobule, but the proximal lobule can also be reduced or the corona can be completely absent, so that the morphological delimitation of the genus is still not finalized.

1. Ditassa thymifolia (Schltr.) Liede & Meve, comb. nov. Basionym: *Orthosia thymifolia* Schltr., Bot. Jahrb. Syst. 54(3, Beibl. 119): 2. 1916. *Cynanchum thymifolium* (Schltr.) Morillo, Ernstia 2(3–4): 69. 1992. TYPE: Peru. Piura: Linkes Seitental des Flusses Huancabamba bei Shumaya, 1700–1800 m, Apr. 1912, *A. Weberbauer 6277* (lectotype, designated by Morillo [1992: 69], US!). Figure 9.

The highly fused corona at first places this taxon in *Orthosia*, as correctly seen by Schlechter (1916). However, after molecular analysis clearly placed the species in Metastelmatinae, and there in *Ditassa*, the vegetative characters of an erect to scrambling shrublet; the small, rigid leaves; and the indument on the adaxial corolla lobes can be interpreted as supportive of a position in *Ditassa*.

Additional specimen examined. PERU. **Cajamarca:** Prov. Chota, Rd. Olmos to Jaén Bagua, E slope of Abra Porculla, 05°50′S, 079°29′W, 2035 m, 4 May 2006, *Weigend, Schwarzer et al. 8606* (B, UBT, USM).

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Appendix 1. List of species.

Ditassa banksii R. Br. ex Schult.
Ditassa thymifolia (Schltr.) Liede & Meve
Jobinia balslevii (Morillo) W. D. Stevens
Jobinia campii (Morillo) W. D. Stevens
Jobinia canoi (Morillo) Liede & Meve
Jobinia chlorantha (K. Schum.) Malme
Jobinia connivens (Hook. & Arn.) Malme
Jobinia eulaxiflora (Lundell) W. D. Stevens
Jobinia fontellana Liede & Meve
Jobinia formosa (N. E. Br.) Liede & Meve
Jobinia glossostemma (Lillo) Liede & Meve
Jobinia grandis (Hand.-Mazz.) Goes & Fontella
Jobinia hatschbachii Fontella & E. A. Schwarz
Jobinia latipes (Decne.) Liede & Meve
Jobinia lindbergii E. Fourn.
Jobinia longicoronata Goes & Fontella
Jobinia mazzuchii (Speg.) Liede & Meve
Jobinia neei (Morillo) Liede & Meve
Jobinia paranaensis Fontella & C. Valente
Jobinia peruviana Liede & Meve
Jobinia samuelssonii (Malme) Liede & Meve
Jobinia schizocorona (Liede & Meve) Liede & Meve
Jobinia streptantha (Malme) Liede & Meve
Jobinia tarmensis (Schltr.) Liede & Meve
Jobinia tiarata (Malme) Liede & Meve
Jobinia trifurcata (Griseb.) Liede & Meve
Jobinia umbellata (Rusby) Liede & Meve
Monsanima morrenioides (Goyder) Liede & Meve
Orthosia angustifolia (Turcz.) Liede & Meve
Orthosia bonplandiana (Schult.) Liede & Meve
Orthosia calycina (Schltr.) Liede & Meve
Orthosia cardozoi (Morillo) Liede & Meve
Orthosia cassythoides (Suess.) Liede & Meve
Orthosia congesta (Vell.) Decne.
Orthosia cynanchoides W. D. Stevens
Orthosia dusenii (Malme) Fontella
Orthosia eichleri E. Fourn.
Orthosia ellemannii (Morillo) Liede & Meve
Orthosia extra-axillaris W. D. Stevens
Orthosia guilleminiana (Decne.) Liede & Meve
Orthosia henriqueana (Silveira) Liede & Meve
Orthosia itatiaiensis Malme
Orthosia kunthii Decne.
Orthosia loandensis Fontella & C. Valente
Orthosia meridensis (Morillo) Liede & Meve
Orthosia parviflora (E. Fourn.) Liede & Meve
Orthosia pearcei (Rusby) Liede & Meve
Orthosia pubescens (Greenm.) Liede & Meve
Orthosia ramosa W. D. Stevens
Orthosia scoparia (Nutt.) Liede & Meve
Orthosia selloana (E. Fourn.) Liede & Meve
Orthosia smaragdina W. D. Stevens
Orthosia stannardii (Morillo) Liede & Meve
Orthosia stenophylla Schltr.
Orthosia stipitata W. D. Stevens
Orthosia umbrosa Decne.
Orthosia urceolata E. Fourn.
Orthosia virgata (Poir.) E. Fourn.
Orthosia woodii Meve & Liede
Scyphostelma beckii (Morillo) Liede & Meve
Scyphostelma bifida (Liede & Meve) Liede & Meve
Scyphostelma brachyphylla (K. Schum.) Liede & Meve
Scyphostelma carmenaemiliae (Morillo) Liede & Meve
Scyphostelma chimboracensis (Morillo) Liede & Meve
Scyphostelma confusa (R. W. Holm) Liede & Meve
Scyphostelma ecuadorensis (Schltr.) Liede & Meve
Scyphostelma filisepala (Standl.) Liede & Meve
Scyphostelma granatensis Baill.
Scyphostelma harlingii (Morillo) Liede & Meve
Scyphostelma intricata (K. Schum.) Liede & Meve
Scyphostelma isidrensis (Morillo) Liede & Meve
Scyphostelma lechleri (Morillo) Liede & Meve
Scyphostelma longecalicina (Morillo) Liede & Meve
Scyphostelma luteynii (Morillo) Liede & Meve
Scyphostelma microphylla (Kunth) Liede & Meve
Scyphostelma nubicola (Morillo) Liede & Meve
Scyphostelma pichinchensis (K. Schum.) Liede & Meve
Scyphostelma ruizteranii (Morillo) Liede & Meve
Scyphostelma serpyllifolia (Kunth) Liede & Meve
Scyphostelma siderocalyx (Morillo) Liede & Meve
Scyphostelma sodiroi (K. Schum.) Liede & Meve
Scyphostelma tenella (L. f.) Liede & Meve
Scyphostelma trianae (Schltr.) Liede & Meve
Scyphostelma veleziae (Morillo) Liede & Meve
Scyphostelma velutina (Morillo) Liede & Meve
Scyophostelma wurdackii (Morillo) Liede & Meve

SEED AND SEEDLING ECOPHYSIOLOGY OF NEOTROPICAL MELASTOMATACEAE: IMPLICATIONS FOR CONSERVATION AND RESTORATION OF SAVANNAS AND RAINFORESTS[1]

Fernando A. O. Silveira,[2,3] *G. Wilson Fernandes,*[3] *and José P. Lemos-Filho*[2]

Abstract

We review the patterns of fruit maturation, dispersal, germination, seed bank formation, and seedling establishment of the Melastomataceae in two Neotropical biodiversity hotspots, the Brazilian cerrado and the Atlantic rainforest. Studies on seed biology of the Melastomataceae are relevant because this family is ubiquitous, species-rich, and dominant in these two hotspots, and its increased relative importance is anticipated under the current scenario of habitat loss and forest fragmentation. The life-history traits of this pioneer-dominated family are quite variable in terms of fruiting phenology and seedling establishment, but less so for dispersal ecology and seed germination. Our knowledge of this seed biology is used to infer on the predicted impacts of global change and forest fragmentation for tropical forest and cerrado melastomes. Species in the Melastomataceae may be key in restoration ecology, and we discuss how seed- and seedling-based restoration techniques can assist ecosystem recovery.

Resumen

Revisamos los patrones de maturación de frutos, dispersión, germinación, banco de semillas y establecimiento de plantas de Melastomataceae en dos hotspots debiodiversdad, el cerrado y la Mata Atlántica. Estudios de semillas de Melastomataceae son importantes porque la familia presenta alta diversidad y es dominante en un gran rango de hábitats. Además, resulta que la familia tiene prevista su importancia aumentada en escenarios de fragmentación de bosques. Las características de história de vida de esta familia de plantas pioneras es muy variable con respecto a la fenología reproductiva y establecimiento de plántulas, pero no tanto con respecto a la ecología de dispersión de semillas y germinación. La biología de semillas embasa la discusión sobre los impactos de los cambios globales y fragmentación de bosques en Melastomataceae de sabanas y bosques tropicales. Especies de Melastomataceae pueden ser claves para la ecología de la restauración y discutimos como las técnicas de restauración basadas en semillas y plántulas pueden ayudar en la restauración.

Key words: Forest fragmentation, global change, Melastomataceae, Neotropics, seed bank, seed dispersal, seedling establishment, seed germination.

Patterns of seed germination have important ecological and evolutionary implications. Germination patterns affect population dynamics, individual fitness (Verdú & Traveset, 2005; Donohue et al., 2010), and species geographic distribution and abundance (Donohue et al., 2010), ultimately leading to changes at the community level. Patterns and processes relative to seed germination have also been used to explain intraspecific competition (Verdú & Traveset, 2005), coexistence of sympatric species (Grubb, 1977), and ecological breadth and geographic range (Donohue et al., 2010), hence highlighting the role of germination in structuring plant communities. Moreover, knowledge of seed biology is integral to our understanding of processes such as plant establishment and natural succession and

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contributes to the development of a theoretical framework for restoration ecology (Vásquez-Yanes & Orozco-Segovia, 1993). Herein, we review the available evidence on seed development, dispersal, predation, germination, and seedling ecophysiology of cerrado and Atlantic forest Melastomataceae. Finally, we briefly discuss how knowledge of seed and seedling ecology of melastomes may be applied to conservation and restoration.

The Brazilian Cerrado and Atlantic Forest

The effects of human activities have considerably diminished the Brazilian cerrado and Atlantic forest in their areas of coverage. The cerrado covers nearly two million km^2, representing 22% of the land surface of Brazil and occupies an altitudinal range from near sea level to 1800 m.s.m. (Oliveira-Filho & Ratter, 2002). The cerrado developed on highly weathered low pH soils, which were aluminum-rich and poor in nutrients (Ratter et al., 1997). The climate is seasonal, marked by dry winters from April to September and rainy summers from October to March (Oliveira-Filho & Ratter, 2002). Typical cerrado vegetation landscape consists of a complex mosaic of savanna physiognomies on well-drained interfluves with riparian forests along watercourses. Physiognomies range from dense grasslands with shrubs and small trees sparsely interspersed (Fig. 1A) to almost closed woodlands (Ratter et al., 1997). Both woody and herbaceous flora developed traits typical of pyrophytic savanna vegetation. The trees are of a low contorted form, with thick, corky, fire-resistant bark and sclerophyllous leaves and underground perennating organs (Simon et al., 2009). Soil erosion, land degradation, uncontrolled fires, and invasive species, along with increases in cleared areas for agriculture, pasture, and charcoal production threaten cerrado biodiversity. Deforestation rates are higher in the cerrado than in the Amazon forest, whereas conservation efforts have been modest: only 2.2% of the cerrado area is currently under legal protection (Klink & Machado, 2005).

The Atlantic forest originally covered ca. one million km^2, extending throughout the Brazilian coast. The biome is composed of two major vegetations: the Atlantic rainforest, which covers mostly the low to medium elevations (< 1000 m.s.m.) along the South American coastline; and the Atlantic semi-deciduous forest that extends toward the west, across the Brazilian plateau in the central and southeastern interior of the continent (Morellato & Haddad, 2000; Oliveira-Filho & Fontes, 2000). The south–north orientation of the coastline and mountain ranges gives rise to orographic rains, resulting in an ever-wet rainforest climate, with annual precipitation exceeding 2000 mm. The relative humidity is higher than 85% year round and the mean annual temperature is nearly 22°C (Morellato et al., 2000). The Atlantic forest has been subjected to intense human pressures, and only a small portion of its original area of coverage remains (ca. 11.4%–16%) as small and isolated fragments (Ribeiro et al., 2009: 1145).

Melastomataceae in the Cerrado and Atlantic Forest

The Melastomataceae comprise shrubs, climbers, herbs, epiphytes, or trees that occur from montane to lowland forests and in savannas and disturbed vegetation (Clausing & Renner, 2001). This pantropical family comprises 4570 species in 150 to 166 genera arranged into nine tribes (Renner, 2004) and attains its highest taxonomic diversity in the Neotropics with ca. 3000 species (Renner et al., 2001). The Melastomataceae is the fourth most speciose family in the cerrado (Mendonça et al., 2008). Melastome diversity is high in both herbaceous and woody communities (Ratter et al., 1997), significant in terms of species number, area of occurrence, aerial cover (Jacobi et al., 2007), and endemism (Romero & Martins, 2002). Representative taxa include the Miconieae, Microlicieae, and Melastomeae (Mendonça et al., 2008). Miconieae, the most species-rich tribe, is a monophyletic tribe characterized by inferior or partly inferior ovaries that develop into baccate fruits (Goldenberg et al., 2008). Nearly 90% of the estimated 275 to 300 species of Microlicieae originated in and are endemic to the cerrado (Fritsch et al., 2004; Simon et al., 2009). Melastomeae is characterized by having stamens with a pedoconnective, appendages ventral and paired when present, and capsular fruits that contain cochleate seeds with curved embryos (Michelangeli et al., 2013). This tribe includes at least 870 species in 47 genera. Most threatened species belong to endemic Microlicieae (Mendonça & Lins, 2000).

The Melastomataceae is amongst the most important families in the woody flora of the Atlantic forest. *Miconia* Ruiz & Pav. and *Tibouchina* Aubl. are the dominant genera in both Atlantic rainforest and semi-deciduous forests (Oliveira-Filho & Fontes, 2000). The family is diverse both in lowland and montane forests in northeastern Atlantic forest (Cavalcanti & Tabarelli, 2004). Gap specialist shrubs and shade-tolerant trees in Melastomeae and Miconieae account for the highest diversity, but species in Bertolonieae and Henrietteae are also important. The Microlicieae is species-poor in the Atlantic forest (Fritsch et al.,

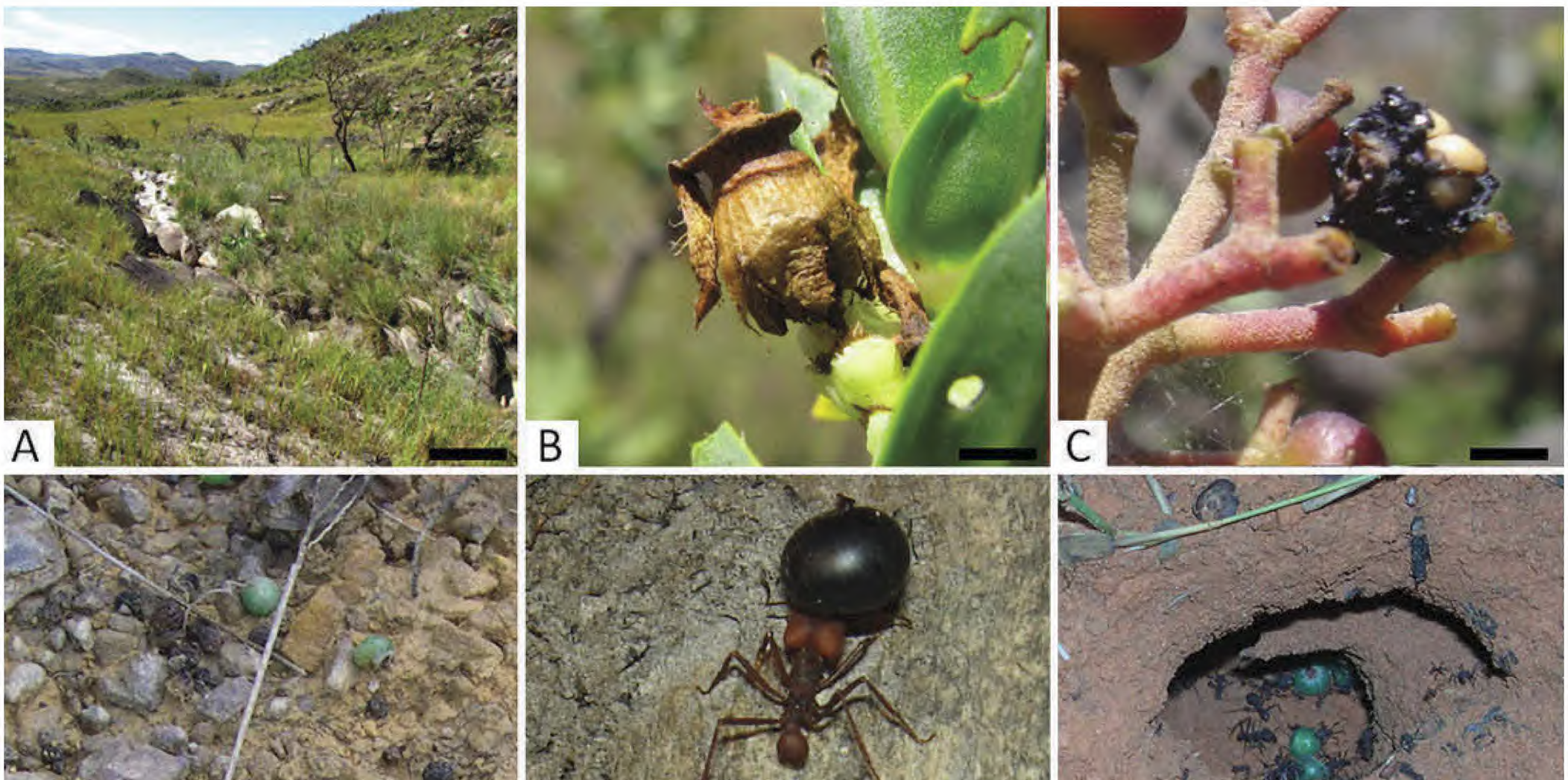


Figure 1. Bird and ant frugivory in *Miconia* Ruiz & Pav. —A. General view of a campo rupestre (altitudinal rocky grassland). —B. Dry capsule of *Lavoisiera confertiflora* Naudin showing the base-to-apex dehiscense. —C. Mashed fruit of *M. irwinii* Wurdack in campo rupestre. —D. Fresh and rotten fruits of *M. albicans* (Sw.) Steud. fallen beneath parent plant. —E. *Atta sexdens* L. soldier carrying *M. irwinii* berry. —F. Fallen fruits of *M. albicans* near *A. sexdens* nest. —G. Attini ant chewing on a fruit stalk. —H. Infructescence of *M. albicans* galled by *Ditylenchus gallaeformans*, leaving no unattacked fruits —I. Early seedling establishment in the campo sujo. Photo of E taken by M. H. C. Lima; all other photos taken by F. A. O. Silveira. Scale bar for A = 1 m, B = 0.4 cm, C–E, I = 1 cm, F = 2 cm, G = 0.5 cm, and H = 2 cm.

2004). New World Melastomeae occupies a variety of forest vegetation types including lowland and cloud forests and some species occupy seasonally flooded habitats (Michelangeli et al., 2013).

FROM FLOWER TO FRUIT

The pollination biology and breeding system of the Melastomataceae have been reviewed by Renner (1989). The Miconieae shows a disproportional occurrence of apomictic species with respect to the other tribes (Goldenberg & Shepherd, 1998; Mendes-Rodrigues & Oliveira, 2012), and seeds obtained from apomictic species are able to germinate normally. Polyembryony is often associated with apomictic widespread species in South America (Mendes-Rodrigues & Oliveira, 2012).

Seeds of the Melastomataceae are small to minute in size and lack endosperm. Mature seeds are exarillate and exalbuminous (Baumgratz, 1985). Most seeds are typically between 0.4 and 2 mm in length, and seed mass is generally less than 0.01 g (an exception is *Mouriri* Aubl., for which fruits are 0.5–10 cm long; Renner, 1989). Fully developed embryos consist of a conspicuous embryonic axis and two fleshy cotyledons (Baumgratz, 1985; Silveira et al., 2012b). The radicles are short and hardly distinguishable from the hypocotyl. Phenolic compounds generally occur in the seed coats, in cell walls, or in the vacuoles (Silveira et al., 2012b). The embryos are

often bent, folded, investing, linear, and/or spatulate (Baskin & Baskin, 2007, Silveira et al., 2012b), and completely fill the seed, resulting in a high embryo to seed ratio (Forbis et al., 2002).

Fruit and seed maturation studies provide the initial basis for understanding germination ecology. Melastomes produce an unusual diversity of fruit types including woody berries, fleshy capsules, and capsules containing fleshy placentas, but for simplicity we refer only to berries and capsules. Melastome capsules and berries have evolved independently several times within the family (Clausing et al., 2000). Fruit character plasticity in the Melastomataceae may relate to shifts in seed dispersal mechanisms, which in turn relate to the type of habitat and dispersal agent. Thus, changes from fleshy berries to dry capsules may correlate with colonization of more open habitats where wind dispersal is more effective than animal dispersal (Clausing et al., 2000). Alternatively, capsular-fruited species may undergo selection for increased exocarp and placenta fleshiness in more closed-forest habitats where vertebrate dispersal predominates (Clausing et al., 2000). Animal-dispersed melastomes are more diverse in forests, whereas capsular-fruited groups are richer in savannas (Stiles & Rosselli, 1993).

The extent of berry maturation (the time between pollination and ripening) greatly varies among the Melastomataceae, with most species showing an irregular pattern of fruit maturation within the canopy and inflorescence (Pereira & Mantovani, 2001). Such a period of fruit and seed maturation may extend from 100 to 220 days after anthesis (DAA) for fleshy-fruited species (Carreira, 2004). In *Tibouchina mutabilis* (Vell.) Cogn., 10% of dry seeds were viable at 14 DAA, and a high percentage of viable seeds was observed 21 DAA (Simão et al., 2007). Mature seeds of *T. granulosa* (Desr.) Cogn. were harvested only between 84 and 105 DAA (Lopes et al., 2005). As for berries, their tissues remain hydrated (70%–80%, water content) and accumulate sugars (Lima et al., 2013). Germination inhibitors occur in unripe and ripe berries of several *Miconia* species (Amaral & Paulilo, 1992; Carreira, 2004; Silveira et al., in prep), which suggests that seed cleaning by frugivores is required prior to germination (Silveira et al, 2012a; Lima et al., 2013). Seed water content at maturity was noted as 27% for *Miconia albicans* (Sw.) Steud. (Carreira, 2004) and 23% for *M. cinnamomifolia* (DC.) Naudin (Lopes & Soares, 2006) and *T. granulosa* (Lopes et al., 2005). Recalcitrance has been reported only for *Melastoma malabathricum* L. from tropical swamp forests (Farnsworth, 2000).

Malformed and well-developed but embryoless seeds (WELS) are commonplace in the family (Baumgratz, 1985). Quantitative data are lacking perhaps because of the difficulty of evaluating viability among the small-seeded species. The percentage of WELS ranges from 13% to 86.5% and varies across lineages including *Tibouchina* (Zaia & Takaki, 1998; Simão & Takaki, 2008; Silveira et al., 2012b), *Trembleya* DC. (Rodrigues & Silveira, 2013), *Miconia* (Mendes-Rodrigues et al., 2010; Silveira et al. 2012b; Silveira et al., in prep.), *Marcetia* DC. (Vasconcelos et al., 2007), *Chaetostoma* DC., and *Comolia* DC. (Silveira et al., 2012b).

From the Mother Plant to Soil

Seed dispersal is strongly influenced by life-history traits and fruit morphology. Fruits are structurally diverse in the Melastomataceae, and dispersal mode varies as a function of fruit morphology (Clausing et al., 2000). Nearly 40% of Neotropical melastomes have capsular fruits, whereas 60% have endozoochorous berries (Renner, 1989). Species in the Miconieae are animal-dispersed, whereas Melastomeae and Microlicieae are abiotically dispersed (Silveira, 2011). Apart from differences in fruit morphology, melastomes are also diverse in their reproductive phenology.

FRUITING PHENOLOGY

In the Amazon forest, reproductive phenology of melastomes tends to occur continuously throughout the year (Renner, 1986–1987, but see Paarmann et al., 2002). However, fruiting phenology in Atlantic forest trees is variable (Morellato et al., 2000), as exemplified by Miconieae. In the lowland Atlantic forest, *Leandra* sp. indet., aff. *sublanata* Cogn. (Gridi-Papp et al., 2004), *Miconia dodecandra* Cogn., and *Tibouchina pulchra* (Cham.) Cogn. fruit year round, whereas *M. prasina* (Sw.) DC., *M. rigidiuscula* Cogn. (Talora & Morellato, 2000), *M. cinnamomifolia* (Mantovani et al., 2003), *M. cinerascens* Miq. (Gridi-Papp et al., 2004), and *M. hypoleuca* (Benth.) Triana (Galetti & Stotz, 1996) fruit only during the dry season (June to August). *Miconia cabussu* Hoehne (Mantovani et al., 2003) and *M. urophylla* DC. (Manhães et al., 2003), in turn, fruit during the rainy season of November to March. The predominant aseasonal fruiting phenology of melastomes in the Atlantic rainforest suggests that climatic factors do not limit fruit production in forest trees. Rather, competition for frugivores may be a stronger selective pressure, and, thus, in the Atlantic forest, fleshy fruits are available year round for frugivores

(Morellato et al., 2000). Staggered fruiting seasons may have competitively evolved in *Miconia* species that share similar animal-dispersal agents (Snow, 1965). Melastome berries are regarded as a key resource for Neotropical frugivorous birds, providing them with otherwise limited water and sugar-based resources (Stiles & Rosselli, 1993; Galetti & Stotz, 1996). Fruiting phenologies of forest *Miconia* from other sites in South America are also segregated over time (Poulin et al., 1999; Kessler-Rios & Kattan, 2012), supporting the hypothesis that segregated fruiting may have evolved through interspecific competition (Snow, 1965).

Within the cerrado, however, seedling establishment is assumed to be constrained during the dry winters, with selective pressure for temporal shifts of reproductive phenophases during the onset of the rainy season. Thus, the synchronization of seed dispersal near or during the onset of the rainy season (that period of high soil moisture) is believed to increase seedling survival and reduce drought-induced mortality (Oliveira, 2008). Unfortunately, there are too few phenological studies on cerrado melastomes (Lopes et al., 2005; Montoro & Santos, 2007; Simão et al., 2007; Garcia et al., 2009) to determine whether fruiting patterns found for forest melastomes are similar to those from the cerrado. There is some preliminary evidence suggesting staggered fruiting in cerrado Miconieae (Maruyama et al., 2007; Silveira et al., unpublished data).

Dispersal Ecology

Data on abiotic dispersal of melastome capsules are scarce. Even though most capsular-fruited melastomes are thought to be wind-dispersed (Silveira, 2011; Fig. 1B), rainfall is needed to release the seeds from the capsules of *Bertolonia mosenii* Cogn. and probably other Bertolonieae (Renner, 1989; Pizo & Morellato, 2002). The distance of the anemochoric dispersal in such melastomes is currently unclear. Berries from riparian *Tococa* Aubl. species that fall into the water and float further into moist forest habitats represent another example of abiotic dispersal. Pubescent seeds may be adaptations to water and/or fish dispersal (Michelangeli, 2005).

Most Miconieae produce small black, red, or blue berries (Renner, 1989). Berries of the Miconieae usually have fleshy placentas and fused tissues or carpels and other accessory structures (Cortez & Carmello-Guerreiro, 2008) in which numerous small seeds are embedded (Silveira et al., 2012b; Lima et al., 2013). Such melastome berries fall into the category of generalist fruits, typically characterized by small size (5–35 mm diam., Renner, 1989), high fecundity, small seed size, and low protein content (McKey, 1975). Such small berries with high water and sugar content are consumed by small frugivorous and omnivorous birds in several families (McKey, 1975; Renner, 1989; Michelangeli, 2005; Schupp et al., 2010; Kessler-Rios & Kattan, 2012).

In Costa Rican, Amazonian, and Atlantic forests, Tyrannidae (fly-catchers), Pipridae (manakins), Turdidae (thrushes), and Thraupidae (tanagers) are major avian frugivores (Loiselle & Blake, 1999). However, the Pipridae are species poor in the cerrado (Macedo, 2002). Large birds in Cracidae (chachalacas, guans, and curassows), Columbidae (doves and pigeons), and Ramphastidae (toucans) play a minor role in fruit removal in South America (Renner, 1989). Fruits of *Mouriri elliptica* Mart., found in the cerrado, are argued to be anachronic (fruits with apparent ex-adaptations to the extinct South American megafaunal community; Guimarães et al., 2008).

The understory melastomes in Costa Rican rainforests have a relatively small set of seed dispersers in contrast to those for canopy trees. Effective dispersers are essentially composed of two or three species, and plant–bird interactions may be more specific in forest understory than in species-rich canopies (Loiselle & Blake, 1999). Brazilian melastome shrubs are visited by a larger assemblage of generalist frugivores (Galleti & Stotz, 1996; Pereira & Mantovani, 2001; Marcondes-Machado, 2002; Manhães et al., 2003; Michelangeli, 2005).

Effects of frugivores on seeds and seedlings

Fruit consumption by frugivores does not necessarily mean that seeds are dispersed because ingested seeds can be damaged by gut passage. The effect of such dispersal can be measured in quantitative and qualitative components (sensu Schupp et al., 2010). Birds are not alike in their ecological roles as seed dispersers for shrubs in the Melastomataceae, differing in both dispersal quantity and quality (Loiselle & Blake, 1999). Removal rates are typically low by manakins and tanagers (Blendinger et al., 2008). The two groups differ in feeding ecology, as the former gulp, eating the fruit whole (high dispersal quantity), and the latter mash and drop seeds near the parent plant (low dispersal quantity; see Fig. 1C) where seed survival is reduced by density-dependent mortality (Stiles & Rosselli, 1993).

Seed cleaning by frugivores improves dispersal quality by removing inhibition factors. The inhibition effect arises from low osmotic potential caused by the high sugar content of ripe fruits, light-blocking pigmentation that prevents enough light reaching

the seeds, and secondary metabolites that directly inhibit seed germination (Samuels & Levey, 2005). Germination inhibitors in fruits of several *Miconia* species (Amaral & Paulilo, 1992; Carreira, 2004) suggest the widespread occurrence of these compounds in the family, though their chemical nature still awaits determination. Seeds within intact melastome fruits (Fig. 1D) rarely germinate (Silveira et al., 2012a), making seed cleaning beneficial for recruitment. Finally, pulp removal may help decrease the probability of pathogen-induced seed death; intact fruits show extensive signs of fungi infestation (Silveira et al., 2012a). The pulp removal and consequent removal of inhibitory compounds are provided by gulpers and to a lesser extent by mashers.

Seed passage through frugivore guts causes differing effects on germination. Seed retention time inside the disperser and the morphology and physiology of its digestive tract may all affect the survival probability of ingested seeds (Traveset el al., 2007). Intact seeds of *Tococa* and *Miconia* have been retrieved after gut passage of fishes (Michelangeli, 2005) and coatis (*Nasua nasua* L., Alves-Costa & Eterovick, 2007), but the lack of germination trials prevents attempts to link dispersal with recruitment. Germinability of seeds from rodent scats was not affected (Lessa & Costa, 2009), but was improved after marsupial gut passage (Lessa & Costa, 2010).

The effects of gut passage of several Costa Rican melastomes after ingestion by the red-capped manakin *Pipra mentalis* Sclater ranged from positive to negative (Ellison et al., 1993). Overall for forest (Manhães et al., 2003; Alves et al., 2008; Gomes et al., 2008) and cerrado species (Silveira et al., 2012a), seed passage through bird gut has minor effects on germination. The seeds of *Clidemia hirta* (L.) D. Don were thought to be dormant, requiring bird ingestion for dormancy break (Pereira-Diniz, 2003). For this species, there was indeed a positive effect of gut passage on germination (Linnebjerg et al., 2009), but data did not support the hypothesis of seed dormancy.

Other primary and secondary dispersers

Birds are the main dispersers of melastomes, but mammals are also important primary seed dispersers. Berries are eaten by bats, monkeys (Renner, 1989; Galleti & Stotz, 1996; de Figueiredo & Longatti, 1997; Garcia et al., 2000; Lapenta & Procópio-de-Oliveira, 2008), rodents, marsupials (Magnusson & Sanaiotti, 1987; Lessa & Costa, 2009, 2010), and coatis (Alves-Costa & Eterovick, 2007). A large portion of the fruit produced by Miconieae is not removed by primary dispersers. Fruits fallen to the ground are eaten by turtles, lizards, tapirs (Renner, 1989), and armadillos (Baumgratz et al., 2006). Nevertheless, ants are the most important seed consumers of fallen fruits (Fig. 1E, 1F). Ants actively forage on soil in search for small-sized diaspores or even climb in the plants to cut fruit stalks (Fig. 1G). Fungus-growing ants (Attini) transport *Miconia* fruits in the cerrado (Christianini & Oliveira, 2009; Lima et al., 2013) and also remove seeds from bird feces (Leal & Oliveira, 1998; Christianini & Oliveira, 2009). Interactions between ants and fallen melastome fruits may be especially common in lowland rainforests in which ant abundance is coupled with year-round availability of fleshy fruits (Dalling & Wirth, 1998; Pizo & Oliveira, 2000).

Potential benefits of ants to non-myrmecochorous melastomes include seed cleaning, increased germination success, reduced damage to seeds and seedlings, and reduced sibling competition (Rico-Gray & Oliveira, 2007). Because seeds within fallen fruits are less likely to germinate (Fig. 1D), pulp removal and subsequent reduction in fungal infestation (Samuels & Levey, 2005; Rico-Gray & Oliveira, 2007) may be an important benefit emerging from ant–melastome interactions. Fruit displacement may increase the chances of seeds reaching safe sites, and seed deposition in refuse piles may provide seedlings with a suitable substrate for establishment (Lima et al., 2013). Because seed delivery patterns by ants are likely to differ from those of birds, ants may influence species population dynamics and spatial distribution (Christianini & Oliveira, 2009).

From Seed to Seedling: Effects of Light and Temperature

Light and temperature are among the most significant abiotic factors controlling seed germination (Heschel et al., 2007). Here, we focus on how melastome seeds respond to these abiotic stimuli. Despite the relatively few species reviewed (29 species in eight genera, Table 1), a general pattern for seed germination in the Melastomataceae emerged. Under controlled conditions, seeds of the 25 species investigated were uniformly and positively photoblastic. Germination of melastome seeds under dark conditions is negligible, irrespective of phylogenetic position, geographic distribution, growth form, or temperature (Silveira, 2011).

Extreme temperatures seem to be deleterious for melastome germination, with only 33% of cerrado species and 40% of Atlantic forest species germinating at temperatures above 30°C (see Table 1). Optimum temperature (which allows faster and maximum germination) is reported for only 62% of

Table 1. The effect of light and temperature on germination of Melastomataceae seeds from Brazilian cerrado and Atlantic forest. *Tibouchina heteromalla* is the only taxon considered from both biomes and *Miconia cinnamomifolia* and *T. granulosa* appear twice because they represent accessions for two different studies.

Biome	Tribe	Species	Maximum G (%)[a]	Temperature range	Optimum temperature	Light response	Dormancy type	Reference
AF	Melastomeae	*Tibouchina benthamiana* (Gardner) Cogn.	~70	20–30	30	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. granulosa* (Desr.) Cogn.	24.9	NA	NA	L > D	ND	Zaia & Takaki, 1998
AF	Melastomeae	*T. granulosa* (Desr.) Cogn.	17	NA	NA	L > D	ND	Lopes et al., 2005
AF	Melastomeae	*T. heteromalla* (D. Don) Cogn. [= *T. grandifolia* Cogn.]	~60	15–35	25–30	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. moricandiana* Baill.	~70	20–30	25	L > D	ND	Andrade, 1995
AF	Melastomeae	*T. mutabilis* (Vell.) Cogn.	~80	15–35	25–30	L > D	ND	Simão & Takaki, 2008
AF	Melastomeae	*T. pulchra* Cogn.	30.9	NA	NA	L > D	ND	Zaia & Takaki, 1998
AF	Melastomeae	*T. sellowiana* Cogn.	NA	NA	30	L > D	ND	Barbosa et al., 1988
AF	Miconieae	*Leandra breviflora* Cogn.	78	NA	NA	L > D	ND	Andrade, 1995
AF	Miconieae	*Miconia chamissois* Naudin	90	NA	NA	L > D	ND	Valio & Scarpa, 2001
AF	Miconieae	*Miconia cinnamomifolia* (DC.) Naudin	58.7	NA	25	L > D	ND	Pereira & Mantovani, 2001
AF	Miconieae	*Miconia cinnamomifolia* (DC.) Naudin	~60	20–30	25–30	L > D	ND	Amaral & Paulilo, 1992
AF	Miconieae	*Miconia urophylla* DC.	~60	NA	NA	L > D	ND	Manhães et al., 2003
CE	Melastomeae	*Marcetia candolleana* A. K. A. Santos & A. B. Martins	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia harleyi* Wurdack	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia macrophylla* Wurdack	1	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia shepherdii* A. B. Martins	2	NA	NA	NC	NC	Vasconcelos et al., 2007
CE	Melastomeae	*Marcetia taxifolia* (A. St.-Hil.) DC.	51	15–30	15–25	L > D	ND	Silveira et al., 2004
CE	Melastomeae	*T. gracilis* (Bonpl.) Cogn.	~75	15–35	25–30	L > D	ND	Carreira & Zaidan, 2007
CE	Melastomeae	*T. heteromalla* (D. Don) Cogn. [= *T. multiflora* Cogn.]	73	15–30	25–30	L > D	ND	Garcia et al., 2006
CE	Melastomeae	*T. papyrus* (Pohl) Toledo	70	NA	NA	NA	ND	Montoro & Santos, 2007
CE	Miconieae	*Clidemia hirta* (L.) D. Don	96	NA	NA	L > D	NC	Pereira-Diniz, 2003
CE	Miconieae	*Miconia albicans* (Sw.) Steud.	~80	15–35	20–30	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia ferruginata* DC.	59.5	NA	NA	L > D	NC	Mendes-Rodrigues et al., 2010
CE	Miconieae	*Miconia paucidens* DC. [= *Miconia langsdorffii* Cogn.]	~65	15–30	25	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia rubiginosa* (Bonpl.) DC.	~30	20–35	25	L > D	NC	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia stenostachya* DC.	~65	15–35	20–30	L > D	ND	Carreira & Zaidan, 2007
CE	Miconieae	*Miconia theaezans* (Bonpl.) Cogn.	98	15–32.5	15–32.5	L > D	ND	Godoi & Takaki, 2007
CE	Microlicieae	*Lavoisiera cordata* Cogn.	~85	15–30	20–30	L > D	ND	Ranieri et al., 2003
CE	Microlicieae	*Lavoisiera imbricata* Cogn.	~35	15–30	25	L > D	ND	Ranieri et al., 2003
CE	Microlicieae	*Trembleya laniflora* (D. Don) Cogn.	16.5	15–30	20	L > D	ND	Rodrigues & Silveira, 2013

Abbreviations: L, Light conditions; D, dark; ND, seed nondormancy; D, dormancy; NC, nonconclusive; NA, data are not available.
[a] Percentages not corrected for viability.

the 29 species. Optimum temperature ranged from 20°C to 30°C, with the variable range of 15°C–32.5°C exhibited by *Miconia theaezans* (Bonpl.) Cogn.. Widespread species (*M. albicans*, *M. stenostachya* DC., and *M. theaezans* in cerrado, *Tibouchina mutabilis* in Atlantic forest, and *T. heteromalla* (D. Don) Cogn. in both biomes) were eurythermic, germinating over broad temperature ranges. However, contrary to predictions of the niche breadth hypothesis (Grubb, 1977), endemic species such as *Trembleya laniflora* (D. Don) Cogn., *Lavoiseria cordata* Cogn. ex Glaz., and *L. imbricata* DC. did not show narrow temperature ranges.

The positive photoblastic response of melastome seeds is typical of small-seeded, pioneer species in the Neotropics with seeds that preferentially germinate under forest gaps (Pearson et al., 2002, 2003a; Daws et al., 2008). The response of seed germination to red and far-red light is mediated by phytochromes. Melastome seeds have phytochrome B (*phyB*), which particularly influences germination under shaded or low-fluence conditions (Godoi et al., 2009). This photoregulator responds to differences in red and far-red wavelengths, as altered by canopy gaps (Casal & Sanchez, 1998); *phyB* affects germination despite a broad range of temperatures (Heschel et al., 2007). In the Atlantic forest, the red to far-red light (R:FR) ratios can drop significantly from 1.21 in open areas to 0.28 under closed canopy (Zaia & Takaki, 1999). Low R:FR light ratios under closed canopy may deter germination, and photoblastic seeds would accumulate in soil seed banks until canopy openings. The R:FR threshold for melastome seeds can be as low as 0.12 for *Miconia argentea* (Sw.) DC. (Pearson et al., 2003b). The amount of daily insolation also influences Melastomataceae germination. Melastome seeds require at least 60 minutes of daily irradiation to germinate (Carreira & Zaidan, 2007).

Effects of Fluctuating Temperatures

Temperature fluctuations may alter the responses of seeds to light such that photoblastic seeds can germinate in darkness when submitted to alternating temperatures (Pearson et al., 2002). Increased germinability of small-seeded species as a response to fluctuating temperature can be predicted because seeds buried at shallow soil depths would experience higher daily thermal fluctuations compared to more deeply buried seeds. Forest gaps would also increase daily temperature fluctuations in upper soil layers, relative to deeper soil, and seeds may cue for this variation (Pearson et al., 2002, 2003b). However, alternating temperatures do not promote germination of Neotropical melastomes nor could daily fluctuations in temperature be a surrogate for the light requirement (Carreira & Zaidan, 2007; Godoi & Takaki, 2007; Simão & Takaki, 2008). Among those species investigated (see Table 1), *Miconia chamissois* Naudin is the only taxon that apparently benefitted from alternating temperatures under optimal light conditions. When alternating daily temperatures include extremes, such as 35°C, germinability of melastomes is not observed (Godoi & Takaki, 2007). Daily variation in temperatures has been shown to favor germination of tropical large-seeded pioneers (Válio & Scarpa, 2001; Pearson et al., 2002), but for Neotropical Melastomataceae, alternating temperatures have a minor role in seedling emergence.

SEED DORMANCY

A completely nondormant seed has the capacity to germinate over a wide range of normal physical environmental factors that include water, oxygen, and appropriate temperature (Finch-Savage & Leubner-Metzger, 2006; Thompson & Ooi, 2013 and references therein). A dormant seed is one that contains a viable embryo but will not germinate under the normal physical conditions that otherwise would be favorable for its germination (Baskin & Baskin, 2004; Hilhorst, 2011). The adaptive significance of seed dormancy is to distribute germination in time and space, so that seedling establishment takes place in circumstances that ensure survival and growth (Fenner & Thompson, 2005; Finch-Savage & Leubner-Metzger, 2006; Heschel et al., 2007).

Plant lineages have independently evolved a variety of mechanisms related to seed dormancy in response to diverse selective pressures (Linkies et al., 2010). Nearly 60% of the species found in tropical rainforests and about 50% of those found in tropical semi-evergreen forests are nondormant. In contrast, more than 70% of savanna seeds are dormant (Baskin & Baskin, 2004). There is no evidence supporting seed dormancy in the Melastomataceae in the Atlantic forest (see Table 1). In the cerrado, however, seed dormancy evolved multiple times in seed-dispersing species during conditions unfavorable for establishment, irrespective of phylogenetic position (Silveira et al., 2012b). Consistently, species fruiting in places and times favorable for seedling establishment produce nondormant seeds (Silveira et al., 2012b). The lack of data on WELS and embryo viability (Hilhorst, 2011) casts some doubt on early and recent reports of dormant seeds in melastomes from rainforests (Ellison et al., 1993; Andrade, 1995; Lopes et al., 2005) and savannas (Pereira-Diniz, 2003; Mendes-Rodrigues et al., 2010).

Seeds of melastomes are physiologically dormant (Baskin et al., 1999; Silveira et al., 2012b). Although there is a layer of lignified cells in the seed coat (Baskin & Baskin, 1998), the seed structure of melastomes does not offer resistance to germination (Cortez & Carmello-Guerreiro, 2008). Further, melastome seeds have fully developed embryos (Forbis et al., 2002) and apparently lack either morphological or morphophysiological dormancies. We adhere to the assertion from Thompson and Ooi (2013) that light is not a dormancy factor, but rather a germination requirement. If photodormancy is considered, then all melastomes produce dormant seeds.

Seed Bank Formation

Melastome seeds are among the most abundant and diverse families in the soil seed bank communities across numerous physiognomies in both cerrado and Atlantic forest (Sassaki et al., 1999; Carreira, 2004; Pereira-Diniz & Ranal, 2006; Medina & Fernandes, 2007). Melastome seeds can be found at several soil depths (Pereira-Diniz & Ranal, 2006) in both dry and wet seasons (Sassaki et al., 1999), which accounts for a significant portion of emergent seedlings. Miconieae and Melastomeae predominate in forest seed banks (Baider et al., 1999), whereas Microlicieae stands out in rupestrian grasslands (Medina & Fernandes, 2007).

Melastome seeds are found in seed banks in degraded areas, secondary growth, and mature forest stands, but the seed density of *Miconia* and *Tibouchina* decreases with increasing forest age (Baider et al., 1999). These species constitute early or pioneer communities, which are essential for the establishment of more shade-tolerant trees and consequent forest regeneration (Baider et al., 1999). Thus, the richness of melastomes in soil seed banks highlights their potential role in ecological restoration.

The typically small-sized seeds of the Melastomataceae may be regarded as the principal factor in high seed longevity, rather than seed dormancy (Thompson et al., 2003). Ease in the burial of smaller seeds would inhibit germination and decrease predation, suggesting a predictable relationship between small seed size and persistence in soil (Milberg et al., 2000; Fenner & Thompson, 2005). Artificially stored melastome seeds demonstrated high longevities (Zaia & Takaki, 1998; Pereira-Diniz, 2003; Carreira, 2004). Melastomes produce large numbers of seeds (more than 1000 fruits/individual) (Galetti & Stotz, 1996; Dalling et al., 1998; F. A. O. Silveira, pers. obs.) in a short period of time (less than two months) and enter tropical seed banks together with other woody pioneer and herbaceous species (Baskin & Baskin, 1998), thus playing an important role in regeneration following disturbance. High seed longevity along with high potential to enter and persist in seed banks and copious fruit production may explain why invasive melastomes such as *Miconia calvescens* DC. and *Clidemia hirta* can be difficult to control (Meyer & Florence, 1996).

Seedling Establishment

Seedling establishment is the most fragile phase in the plant's life cycle. Understanding how seedlings respond to both biotic and abiotic stresses is crucial for the conservation and management of plant populations and for ecological restoration. One would expect remarkable differences in recruitment between cerrado and Atlantic forest species of the Melastomataceae because these habitats provide such contrasting conditions for the establishment phase. Studies on melastome seedling establishment are rare; therefore, the following discussion is based on studies from the rainforests of Central America as well as those few studies conducted for cerrado species.

Early accounts of germination and establishment of woody plants in the cerrado indicate little success of sexual reproduction under laboratory conditions in spite of the high proportion of viable seeds and good germinability (Oliveira, 2008). These initial studies were based on observations that a high proportion of species in the community is able to reproduce vegetatively, suggesting that fire-induced mortality would limit the role of regeneration from seeds (Fig. 11). Here, we discuss how drought, fire, cover effects, and interspecific competition impact seedling establishment in the cerrado.

Water shortages during the dry season limit establishment of seedlings to intervals of sufficiently high soil moisture (Salazar et al., 2011). Root systems of seedling and juvenile plants restrict to upper layers of soil in initial development and therefore lack access to available water from deeper soil layers during the dry season (Goldstein et al., 2008). Melastome seeds may germinate in September, but drought-induced mortality in the early wet season may select for delayed germination until the arrival of consistent rainfall during the mid-rainy season (Pereira-Diniz & Ranal, 2006). High soil evapotranspiration at the onset of the rainy season may prevent water from penetrating the lower soil layers; constant irrigation positively increased seedling establishment of *Miconia albicans* (Hoffmann, 1996). For this species, recruitment begins in December, peaks in February, and decreases as the dry season proceeds (Carreira, 2004). Establishment during the mid-rainy

season is an effective strategy to ensure seedling growth and root elongation, resulting in the typical low shoot to root ratio of cerrado species in central Brazil (Hoffmann & Franco, 2003). The higher biomass allocation to roots allows the plant to access deeper soil layers where moisture remains accessible, even after several months without rains (Goldstein et al., 2008).

Fire may also be selective for melastome seedling establishment during the rainy season. Fire negatively affects sexual reproduction, destroys reproductive structures, decreases size-specific reproductive output, and kills seedlings (Hoffmann, 1998). Forest species are fire-sensitive, whereas most cerrado species resprout after fire (Hoffmann, 2000). Fire-induced mortality is particularly costly for small-seeded species, killing 100% of 2-year-old *Miconia albicans* seedlings (Hoffmann, 1998). Thus, seedling establishment of *M. albicans* and *Clidemia sericea* D. Don. peaks in the second and third year after fire (Miyanishi & Kellman, 1986).

Cover effects on seedling establishment in the Melastomataceae include canopy shading and litter cover. Canopy shading is usually neglected as a limiting factor in the cerrado, but potentially restricts seedling growth during early establishment even in open grasslands, noted particularly for cerrado woodlands (Franco, 2002; Goldstein et al., 2008). The grass layer reduces up to 70% of photosynthetic photon flux densities (Franco, 2002) and is likely to alter R:FR light ratios, hence hampering regeneration from seed. Ground litter modifies conditions on the soil surface by intercepting light, reducing thermal amplitude, releasing nutrients and toxins, and reducing evaporation (Fenner & Thompson, 2005). In woodlands, litter may prevent the establishment of *Miconia*. In open grassland, however, scant litter positively affects establishment by reducing soil temperature and desiccation (Hoffmann, 1996).

Finally, grass root competition for water is critical during the wet season in the cerrado, even though topsoil layers remain wet most of the time. Low shoot to root ratio and biomass allocation to roots (Goldstein et al., 2008) allows roots to reach moist soil layers beyond the grass root zone. Also, the buildup of underground energy reserves facilitates regrowth of aerial biomass after fire or drought (Franco, 2002). We lack information on whether the lower amount of melastome seed reserves would limit seedling root growth, thereby affecting competition with grass roots.

Recruitment in forests drastically differs from that in savannas. The closed rainforest canopy alters light quality and quantity (Zaia & Takaki, 1998), thereby hindering regeneration from photoblastic seeds. The light-requiring melastome seeds accumulate in the seed banks and germination is prevented unless canopy gaps occur. Small-seeded species respond to an irradiance cue for germination, while larger-seeded pioneers respond positively to increasing diel temperature fluctuations (Pearson et al., 2002). Despite low survival success (less than 5%), *Miconia* seedlings are 20-fold more abundant in gaps than in understory, with emergence increasing with gap size (Ellison et al., 1993). Because canopy gaps reduce soil moisture (Ellison et al., 1993), seedling mortality in gap-induced dry soils should select for germination in suitable microsites within the gap. Melastomes preferentially recruit in litter-free microsites (Metcalfe et al., 1998; Dalling & Hubell, 2002) as a thicker litter affects light penetration and reduces the R:FR light ratios to inhibitory levels for germination (Pearson et al., 2003a). Melastome seedlings are unevenly distributed within gaps, known to be frequent in root pit and mound microsites (Ellison et al., 1993). Small-seeded species germinate only in comparatively moist microsites as presented by small canopy gaps, which may reduce the risk of drought-induced mortality (Daws et al., 2008).

Interactions with Seed Pathogens, Predators, and Micorrizhae

Melastome fruit and seed interactions with fungi and seed predators are poorly known, despite their ecological and applied relevance. The available studies indicate a great diversity of pre- and post-dispersal seed predators and pathogens in Neotropical melastomes. At least seven seed-feeder species of *Notiobia* (Carabidae) beetles are associated with fallen fruits of *Bellucia* Neck. ex Raf., *Loreya* DC., and *Miconia* in the Amazon (Paarmann et al., 2002). A recently described species of *Allorhogas* (Hymenoptera: Braconideae) induces galls in 15%–58% fruits of *Conostegia xalapensis* (Bonpl.) D. Don, severely decreasing fruit size and seed number (Chavarría et al., 2009). Two species of *Ditylenchus* (Tylenchida: Anguinidae) induce galls in leaves and fruits of cerrado (Viana et al., 2013) and Atlantic forest (Santos et al., 2012) Melastomataceae (Oliveira et al., 20132). Such nematode galls drain photosynthate, destroy infructescences, or both, affecting plant fitness (Viana et al., 2013; Fig. 1H). Their widespread occurrence in the Miconieae (Oliveira et al., 2013) suggests unnoticed negative consequences of nematode-induced galls in the reproduction of native species (Santos et al., 2012; Viana et al., 2013). The overall effect of seed pathogens and predators in recruitment of melastomes is currently unknown, but antagonists have been suggested as

Table 2. Germinability (%) of *Comolia sertularia* (DC.) Triana and *Microlicia tetrasticha* Cogn. seeds under different light and temperature conditions. Four replicates of 25 seeds for each species were set to germinate under conditions of a 12-hour photoperiod (12 hours of light, followed by 12 hours of darkness) and continuous dark (24 hours). Temperatures were held constant at 15°C, 20°C, 25°C, and 30°C, respectively, for 30 consecutive days. Dashes (—) indicate that data were not available. Original data by the authors.

		Germinability (%)							
		15°C		20°C		25°C		30°C	
Species	Year of collection	Light	Dark	Light	Dark	Light	Dark	Light	Dark
C. sertularia	2001	0	0	1	0	3	2	—	—
C. sertularia	2002	0	0	1	0	0	0	1	0
M. tetrasticha	2001	2	0	0	0	0	0	—	—

agents of biological control of invasive melastomes (Seixas et al., 2004; Oliveira et al., 2013).

Fungal and oomyceteous pathogens are major causes of seed mortality for some *Miconia* (Dalling et al., 1998) and may decrease recruitment from seed banks. On the other hand, the occurrence of mycorrizhae in the Melastomataceae may be underestimated and their potential in increasing establishment has been overlooked (Metcalfe et al., 1998; Urcelay et al., 2005; Matias et al., 2009). Nothing is yet known about the role of fungal endophytes in seed and seedling ecology of melastomes.

Seed Ecology of Melastomes in a Changing World

effects of global change

Global climate change effects on germination are speculative since responses are species specific (Fenner & Thompson, 2005), and, thus, the following discussion should be viewed with caution. Regeneration from seed is often expected to benefit from climate warming, perhaps because studies focused on colder regions of the globe (Fenner & Thompson, 2005). Although no study tested the effects of elevated CO_2 and temperature on melastome germination, we predict a negative impact of temperature raise on regeneration from seed banks because melastome germination is disfavored at high temperatures (Tables 1 and 3, Silveira, 2011).

Data forecast a 10%–20% reduction in precipitation in both savannas and rainforests during the dry season (IPCC, 2007). Conversion of cerrado to grasslands increases mean surface air temperature and the frequency of dry periods within the wet season (Hoffmann & Jackson, 2000), changes that could be damaging to melastome seedlings. Despite the effects of changes in precipitation being difficult to predict (Fenner & Thompson, 2005), they will likely constrain melastome recruitment through a predicted shortened rainy season and decreased soil moisture (see Table 3). The intensification of fire frequency may further impact recruitment. Enlarged fire seasons can be detrimental to ecotone-colonizing plants at cerrado–forest boundaries.

Finally, climate change may indirectly disrupt fruit–frugivore interactions by simultaneously reduc-

Table 3. Predicted effects of ongoing human activities on the life cycle transitions of Neotropical Melastomataceae. Plus sign (+) indicates beneficial effects; minus sign (–) reflects deleterious effects; zero (0) indicates neutral, and a question mark (?) indicates unpredictable response.

	CO_2 increase	Temperature rise	Fire increase	Precipitation decrease	Habitat fragmentation
Seed production	?	?	–	–	?
Bird dispersal distance	0	?	0	–	–
Ant dispersal distance	0	?	0	0	–
Seed rain	0	?	0	–	?
Wind dispersal	0	0	0	0	?
Ant–fruit interactions	0	0	–	0	–
Germinability	?	–	–	–	+
Germination time	?	?	–	–	0
Seed bank dynamics	?	–	–	–	+
Seedling establishment	?	–	–	–	–
Seedling herbivory	–	–	0	0	–

ing bird distribution range and promoting frugivore extinction (see Table 3). One estimate predicts that nearly 80% of Amazon manakins would lose their habitable area, and 20% of cerrado manakin species would face extinction under future climate changes (Anciães & Peterson, 2006).

Effects of Habitat Fragmentation

The increasing and unprecedented deforestation level is creating a landscape of edge-dominated forests where edges are more illuminated, desiccated, and wind-exposed than forest interior. Microclimatic alterations change the structure of forest communities, driving the forest fragments toward early-successional conditions (Tabarelli et al., 2008). Pioneer-dominated plant assemblages in forest edges are markedly different in terms of tree species richness and proportion of pioneer and large-seeded species compared to the forest interior (Silva et al., 2007; Santos et al., 2008). A dramatic shift in the plant community in the Atlantic forest toward small-fruited and capsule-bearing species (Silva & Tabarelli, 2000) results from forest fragmentation, selective logging, and hunting pressure, leading to local extinction of large-fruited trees and the movement of large fruit-eating vertebrates out of the region. The apparent success of small-seeded species in disturbed habitats must be assessed in the long term to accurately determine how the melastomes will respond to fragmentation in defaunated areas.

Bird response to fragmentation and consequences for melastome recruitment

Mechanisms determining bird distribution in edges versus forest interior include changes in microclimate, distribution of suitable habitats, parasites and predators, and resource-driven mechanisms (Restrepo & Goméz, 1998). Fragmentation changes bird abundance, richness, and behavior (e.g., movement patterns and fruit consumption), and no general pattern of bird responses to fragmentation emerges because anthropogenic disturbances influence the distribution of understory birds in complex ways (Restrepo & Goméz, 1998; Restrepo et al., 1999; Galetti et al., 2003; Martensen et al., 2008). The result is an altered bird community structure and composition in fragmented areas compared to pristine areas (Restrepo & Goméz, 1998).

Few studies have looked at the fragmentation effects on seed rain, but birds may be unresponsive to changes in fruit abundance in edges versus forest interior (Levey, 1990; Restrepo et al., 1999). Changes in the distribution and survival of frugivores suggest that seed delivery may be reduced in fragments, leading to changes in fruit removal rates as well as the structure and location of edges over time (Restrepo & Goméz, 1998; Galetti et al., 2003). Theoretically, the demography of generalist bird-dispersed small-seeded species, such as Melastomataceae and Rubiaceae, can be affected by fragmentation (Galetti et al., 2003). Because melastome species account for nearly 20% of fruit–frugivore interactions in the forest edge, secondary growth, and also in the canopy and understory of mature Atlantic forests (Silva et al., 2002), the impact should be noteworthy.

Negative effects of fragmentation on fruit removal are not unequivocal (Restrepo et al., 1999). The probability of fruit consumption is lower in the interior than at the edge and in small rather than in large fragments (Galetti et al., 2003). Conversely, higher seed rain of small-sized seeds at the northeastern Atlantic forest edge explains continuous recruitment (Melo et al., 2006). In Central American melastomes, removal rates are higher in young-secondary forest than in old-growth forest regardless of where plants grew. This was associated with higher sugar concentration in berries from young-secondary forest compared to those in old-growth forest species (Lumpkin & Boyle, 2009). Fragmentation effects on seed rain are complex perhaps because of diversity of plant functional types in species-rich tropical forests, but decreased seed dispersal does not necessarily lead to lower recruitment (Valdivia & Simonetti, 2007).

Large fruit–frugivore networks in the Atlantic forest may provide resilience to disturbance (Silva et al., 2007). Forest fragmentation is thought to favor small-seeded species (Silva & Tabarelli, 2000), and, thus, melastomes may not be negatively affected in the short term. Small-seeded plant species are favored because of the dominance of small, habitat-generalist birds. Most of the melastome seed dispersers do well in degraded areas (Pizo, 2007), and disruption of fruit–frugivore mutualism may have only minor effects. Bird distribution is edge-age dependent, so it can be reasoned that time-lag responses may have gone undetected. Additionally, increased fire frequency will likely prevent seedling establishment in forest edges.

Ant response to fragmentation and consequences for melastome recruitment

Ants can be relevant fruit rescuers in sites impoverished of vertebrate dispersal assemblages, and in fragmented or heavily hunted habitats (Christianini & Oliveira, 2009). Therefore, as habitat loss and fragmentation reduce abundance and richness of frugivorous birds, the relative importance

Table 4. The advantages and disadvantages of using Melastomataceae in the most recommended ecological restoration techniques (see text for references to the exemplar recommended techniques).

Restoration technique	Advantage	Disadvantage
Fire protection	a fire-free environment is likely to increase recruitment because of seed and seedling fire sensitivity	may be implicated in problems with farmers, requiring pre-action, social mobilization
Perching	profuse berry production is attractive for a wide range of taxonomic vertebrates, nucleation enhancement, and low cost of implementation	none
Seed rain management	large production of long-lived seeds, low cost for seed rain collection	no control of final seedling number
Seed sowing	copious seed production and low cost for seed collection, handling, and sowing	low seedling recruitment; no control of final seedling number
Litter and soil seed bank management	ubiquity and abundance of melastome seeds in tropical seed banks	may decrease regeneration in nearby fragments
Seedling resprout	very limited technique	melastome studied to date are obligate seeders following disturbance
Seedling transplanting	high seed production and rapid early seedling growth, which ensures control of final seedling number	relatively elevated costs for seedling production

of secondary dispersal by ants increases. Leaf-cutting ants (*Atta* and *Acromyrmex*), the major seed-harvesting ants (Dalling & Wirth, 1998; Leal & Oliveira, 1998; Christianini & Oliveira, 2009; Lima et al., 2013), appear to benefit from fragmentation. Colonies of *Atta sexdens* L. and *Atta cephalotes* L. are more frequently found in forest edges and second-growth forest regeneration patches than in the forest interior as a consequence of shifts in both bottom-up and top-down control (Silva et al., 2009). However, increased herbivory by leaf-cutting ants in the forest edge has also been documented (Urbas et al., 2007; Silva et al., 2009). In highly disturbed sites, colony density increases, but foraging areas of colonies is dramatically reduced compared to forest interiors (Urbas et al., 2007), suggesting that fragmentation indirectly reduces ant dispersal distance (Table 3). Seed harvesting by ants in disturbed areas would restrict seed dispersal to short distances, promote seed clumping, and reduce seedling survival beneath parents, overcoming any positive benefit plants would derive from seed dispersal by ants (Guimarães & Cogni, 2002; Silva et al., 2007).

IMPLICATIONS FOR RESTORATION

Ecological restoration is a high-priority issue in the conservation agenda for Neotropical hotspots. Here, we discuss how the ecology of melastomes can assist seed- and seedling-based restoration approaches (Rodrigues et al., 2009). First, the small-sized fruits of melastomes contain a high number of seeds and are produced year round. This has three key implications for restoration (Table 4): (1) high seed availability does not prevent seedling density improvement and enrichment through seed sowing; (2) berries are attractive to a diverse community of generalist frugivores that deliver seeds from other species to nucleated sites; and (3) transplanted berry-fruited melastomes can surrogate the use of artificial perches and act as stepping stones in fragmented areas.

Second, melastomes are abundant and diverse in tropical soil seed banks (see Seed Bank Formation), allowing transference of litter and soil seed bank from nearby conserved sites. Finally, melastome seedlings have high growth rates (Carreira & Zaidan, 2003; Ranieri et al., 2005), increasing soil coverage and conservation. The inoculation of mycorrhizae and *Rhizobium* promotes increased survival and growth of *Tibouchina heteromalla* (Matias et al., 2009), and can be an alternative for sapling limitation (Table 4).

Melastomataceae are able to colonize degraded areas and create suitable conditions for the establishment of secondary and late-successional species, even in areas with soils contaminated with heavy metals (Jacobi et al., 2007; Rodrigues & Silveira, 2013). They also interact with a wide diversity of pollinators and seed dispersers, and can assist in restoring ecological interactions and ecosystem services. However, melastomes are sensitive to fire and may have a limited role in forest restoration during advanced successional stages. We hope our efforts encourage their use in future ecological restoration programs.

Conclusions

Current data reveal the following findings: (1) capsules are dispersed during the dry–wet transition season, whereas berries are produced year round; (2) tanagers, manakins, and thrushes are the major seed dispersers, but a broad range of bird species also are important in providing seed cleaning and in transporting fruits away from parent plants; (3) ants are dominant secondary seed dispersers, with important benefits arising from their interaction with berries; (4) the small-sized seeds are light demanding, long lived, and accumulate in soil seed banks; (5) physiological dormancy evolved in the cerrado but not in the Atlantic forest; (6) litter abundance, gap size, and within-gap microsite can affect regeneration from seed in forests, whereas fire and drought are determinant for establishment in the cerrado; and (7) fruit traits of Melastomataceae can assist seed-based restoration ecology techniques.

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THE GENUS *CARAPICHEA* (RUBIACEAE, PSYCHOTRIEAE)[1]

Charlotte M. Taylor and Roy E. Gereau[2]

Abstract

The Neotropical species that have been included in *Psychotria* L. comprise a heterogeneous group, morphologically and systematically. *Carapichea* Aubl. (Rubiaceae, Psychotrieae) was separated from *Psychotria* based on molecular analyses to include *C. affinis* (Standl.) L. Andersson, *C. guianensis* Aubl., and *C. ipecacuanha* (Brot.) L. Andersson; two more species were later included based on morphological characters, *C. ligularis* (Rudge) Delprete and *C. lucida* J. G. Jardim & Zappi. Here *Carapichea* is reviewed morphologically and circumscribed to include 23 Neotropical species found from Nicaragua to southeastern Brazil that share characters of the stipules and inflorescence arrangement. The genus is diagnosed mainly by its distinctive stipules, while pyrene characters, previously considered characteristic for the genus, actually vary widely. A revised morphological description of the genus includes more variation than previously documented, which is outlined in the key to species. Seven informal species groups are separated and characterized, and the following new nomenclatural combinations are made here: *Carapichea adinantha* (Standl.) C. M. Taylor, based on *Retiniphyllum adinanthum* Standl. and the sole species of *Stachyococcus* Standl., which fully synonymizes *Stachyococcus* with *Carapichea*; *Carapichea altsonii* (Sandwith) C. M. Taylor, based on *Cephaelis altsonii* Sandwith; *Carapichea araguariensis* (Steyerm.) C. M. Taylor, based on *P. araguariensis* Steyerm.; *Carapichea crebrinervia* (Standl.) C. M. Taylor, based on *Cephaelis crebrinervia* Standl.; *Carapichea fimbriflora* (Steyerm.) C. M. Taylor, based on *P. fimbriflora* Steyerm.; *Carapichea franquevilleana* (Müll. Arg.) C. M. Taylor, based on *P. franquevilleana* Müll. Arg.; *Carapichea klugii* (Standl.) C. M. Taylor, based on *P. klugii* Standl.; *Carapichea maturacensis* (Steyerm.) C. M. Taylor, based on *P. maturacensis* Steyerm.; *Carapichea necopinata* (Standl.) C. M. Taylor, based on *P. necopinata* Standl.; *Carapichea nivea* (Sandwith) C. M. Taylor, based on *Cephaelis nivea* Sandwith; *Carapichea pacimonica* (Müll. Arg.) C. M. Taylor, based on *P. pacimonica* Müll. Arg.; *Carapichea panurensis* (Müll. Arg.) C. M. Taylor, based on *Mapouria panurensis* Müll. Arg.; *Carapichea sandwithiana* (Steyerm.) C. M. Taylor, based on *Cephaelis sandwithiana* Steyerm.; *Carapichea tillettii* (Steyerm.) C. M. Taylor, based on *P. tillettii* Steyerm.; *Carapichea urniformis* (Steyerm.) C. M. Taylor, based on *P. urniformis* Steyerm.; and *Carapichea vasivensis* (Müll. Arg.) C. M. Taylor, based on *Mapouria vasivensis* Müll. Arg. Newly described here is *Carapichea verrucosa* C. M. Taylor of Amazonian Peru, Colombia, and Brazil, which is notable for its relatively large, abaxially (i.e., dorsally) verrucose pyrenes.

Key words: Bolivia, Brazil, *Callicocca*, *Carapichea*, *Cephaelis*, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, IUCN Red List, Nicaragua, Panama, Peru, *Psychotria*, Psychotrieae, Rubiaceae, *Stachyococcus*, Surinam, *Uragoga*, Venezuela.

The Neotropical genus *Carapichea* Aubl. was described for a single species, *C. guianensis* Aubl., that was noted to be very similar to *Psychotria* L. (Rubiaceae, Psychotrieae; Aublet, 1775). *Carapichea* was originally separated from *Psychotria* based on inflorescence features, but was subsequently included by most authors in *Psychotria* or in the related genus *Cephaelis* Sw. Recent molecular systematic studies of *Psychotria* and related genera have significantly changed our understanding of relationships within the tribe Psychotrieae. These studies showed in particular that several morphological characters used to distinguish these genera are actually highly homoplasious (Nepokroeff et al., 1999; Andersson, 2002b). Based on these molecular data, the circumscription of *Psychotria* has been narrowed (Andersson, 2002b); the circumscription of *Palicourea* Aubl. has been expanded (Andersson, 2002b; Taylor & Gereau, 2010); and several genera have been separated from *Psychotria*. *Ronabea* Aubl. is now included in the tribe Lasiantheae (Taylor, 2004); *Coccochondra* Rauschert is included in Psychotrieae but its relationships are not clear (Taylor, 2011); and *Notopleura* (Benth. & Hook. f.) Bremek. (Taylor, 2001a), *Margaritopsis* Griseb. (Andersson, 2001; Taylor, 2005), and *Carapichea* (Andersson, 2002a) are included in Psychotrieae and apparently related to *Palicourea*.

Andersson (2002a, 2002b) separated *Carapichea* based on a broad molecular survey of world Psychotrieae and included in it three species that he studied with molecular data, *C. affinis* (Standl.) L. Andersson, *C. guianensis*, and *C. ipecacuanha* (Brot.) L. Andersson. Subsequently, two other species were

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added to *Carapichea* based on morphological characters: *C. ligularis* (Rudge) Delprete (Delprete, 2003) and *C. lucida* J. G. Jardim & Zappi (Jardim & Zappi, 2008). Here *Carapichea* is reviewed and its circumscription expanded to include 23 Neotropical species, based on morphological survey across the Neotropical species of Psychotrieae. Its taxonomy and morphology in this broadened circumscription are detailed as part of the ongoing study of the systematics of the Neotropical Psychotrieae (e.g., Taylor, 1996, 1997a, 2001a, 2005, 2011; Taylor & Gereau, 2010): the separation of *Carapichea* further clarifies the limits and characteristics of *Psychotria*, *Palicourea*, and related Neotropical genera.

Taxonomic History of *Carapichea*

The genus *Carapichea* was described by Aublet for one species from French Guiana, *C. guianensis* (Aublet, 1775), and Andersson (2002a) summarized its taxonomic treatment by subsequent authors. *Carapichea* was originally described as related to *Psychotria* and was distinguished from the latter genus by its combination of 5-merous flowers and terminal, capitate, pedunculate inflorescences enclosed by a pair of well-developed involucral bracts with acute apices. Generally taxonomists in the 19th and early 20th centuries included within *Psychotria* the species of Psychotrieae with small white flowers borne in branched inflorescences and separated the species with capitate inflorescences enclosed by well-developed involucral bracts variously in *Cephaelis*, *Uragoga* L. ex Baill., *Callicocca* Schreb., and/or *Carapichea*. In the same work, Aublet also described two other genera with capitate inflorescences enclosed by well-developed involucral bracts, *Tapogomea* Aubl. and *Evea* Aubl. *Tapogomea* included five species, all similar to *Carapichea*; *Tapogomea* apparently differed primarily in its inflorescences enclosed by external bracts with obtuse to truncate apices, in contrast to acute apices in *Carapichea*. *Tapogomea* is today considered a synonym of *Psychotria* subg. *Heteropsychotria* Steyerm. (Steyermark, 1972). *Evea* differed markedly from *Carapichea* in its 4-merous flowers and axillary inflorescence position (i.e., with inflorescences borne in both axils of the node). Aublet classified *Evea* together with *Coussarea* Aubl. and *Faramea* Aubl., based on its aristate stipules, 4-merous flowers, and fruits with a single thin-walled seed, which clearly distinguish it from *Psychotria* and related genera; *Coussarea* and *Faramea* are today included in a separate tribe from *Psychotria*, the Coussareeae (Bremer & Eriksson, 2009). *Evea* included only one species, *E. guianensis* Aubl., which clearly belongs to *Faramea* and is today treated as *F. guianensis* (Aubl.) Bremek. (Bremekamp, 1934; Boom & Delprete, 2002). However, some authors subsequently considered *Evea* to be closely related to *Psychotria* (e.g., de Candolle, 1830; Hooker, 1873; Schumann, 1891; Standley, 1916), which has generated some taxonomic confusion.

Swartz (1788) published the name *Cephaelis* for plants similar to *Psychotria*, but separated from the latter genus by their capitate inflorescences with well-developed involucral bracts. He included in *Cephaelis* four species from the Antilles and northern South America, two that were previously described and two that he described as new. The characters that distinguished *Cephaelis* were basically the same as those of *Carapichea* and *Tapogomea*, but Swartz did not explain its distinction from Aublet's genera even though he was familiar with them; one of the species he transferred to *Cephaelis* was *T. violacea* Aubl. In the following century and a half, the name *Cephaelis* was much more widely though incorrectly used than either of Aublet's older names, and subsequently the name *Cephaelis* was conserved with respect to *Carapichea*, *Tapogomea*, and *Evea* with its type conserved as *Cephaelis muscosa* (Jacq.) Sw. (McNeill et al., 2012).

Schreber (1789) published the name *Callicocca* for those species that Aublet (1775) had described variously in *Carapichea*, *Evea*, and *Tapogomea*; thus the name *Callicocca* is illegitimate because it was offered as an unnecessary substitute name when a previously published name should have been used. However, Schreber did not name any species in this genus or otherwise designate a type for *Callicocca*.

The genus name *Ipecacuanha* Arruda and its single species *I. officinalis* Arruda have been widely cited as synonyms of *Carapichea ipecacuanha* (e.g., Andersson, 2002a) and usually designated as illegitimate superfluous names. Arruda did not cite any previously published name, but clearly intended to name a new species. Unfortunately, he gave no descriptive information beyond the observation that this species is cultivated, and thus his names are nomina nuda. Rafinesque (1838) later independently published the name *Ipecacuanha* Raf., with one species, *I. fusca* Raf. Rafinesque noted that *I. fusca* included plants that had been called *Callicocca ipecacuanha* Brot., *Psychotria emetica* L. f. [= *Ronabea emetica* (L. f.) A. Rich.], and *Cephaelis emetica* (L. f.) Pers., but which Rafinesque considered a distinct species.

De Candolle (1830: 532–536) recognized *Cephaelis* and *Carapichea* as separate genera, and he synonymized *Callicocca* and *Evea* with *Cephaelis*. However, he commented that perhaps *Carapichea*

also should be included in *Cephaelis* and separated it only provisionally based on its "subexserted" anthers and stigmas together with its pyrenes that are smooth abaxially (i.e., dorsally) in contrast to the anthers included, the stigmas exserted, and the pyrenes ribbed abaxially in *Cephaelis*. The separation of these two genera by their anther and stigma position is problematic because many if not most species of both genera are distylous: each individual species includes both plants with long-styled (i.e., pin) flowers and plants with short-styled (i.e., thrum) flowers. However, distyly was not yet understood in 1830, and de Candolle separated the long-styled and short-styled flower forms of a single species taxonomically in some other cases as well (e.g., the long-styled and short-styled plants of *Psychotria bahiensis* DC. were included in separate varieties; de Candolle, 1830: 509). De Candolle's separation of *Carapichea* from *Cephaelis* was also problematic because the fruits of several of the species he included in both of these genera were unknown. De Candolle included two species in *Carapichea*: *Carapichea guianensis* with entire stipules, to which he gave the illegitimate new name *Carapichea aubletii* DC., and *Carapichea patrisii* DC. with bilobed stipules, which was subsequently synonymized with *P. hoffmannseggiana* (Willd. ex Roem. & Schult.) Müll. Arg. (Steyermark, 1972).

Contemporaneously Richard (1830: 174–175) in his review of the Rubiaceae differed from de Candolle in his classification of these genera. Richard synonymized both *Carapichea* and *Callicocca* under *Cephaelis*, even though *Carapichea* was the older name and thus had priority. He separated *Cephaelis* from *Psychotria* based only on inflorescence structure: compact and headlike or capitate in *Cephaelis* in contrast to openly or loosely branched in *Psychotria*.

Hooker (1873: 127) separated *Cephaelis* from *Psychotria* similarly to Richard, by its headlike or capitate inflorescences with well-developed involucral bracts, in contrast to openly or loosely branched inflorescences with small bracts in *Psychotria*. Hooker also synonymized several names similarly under *Cephaelis*, including *Carapichea*, *Evea*, and *Callicocca*, even though some of the synonymized names are older. He circumscribed *Psychotria* broadly otherwise, to include a number of species that today are classified variously in *Psychotria*, *Palicourea*, and other genera.

Baillon (1879a) intended to resurrect the name "Uragoga" as an overlooked Linnean name that should be used in place of several other generic names, but instead Baillon published *Uragoga* L. ex Baill. under his own authorship because Linnaeus (Linné, 1737) only used that name, spelled as "Ouragoga," in a work published before the 1753 starting date for botanical nomenclature (McNeill et al., 2012), so Linnaeus's name was not validly published. Therefore, *Uragoga* was not effectively published until 1879 and does not have nomenclatural priority over most of the genus names for this group. The publication of the name *Uragoga* is attributed to Baillon's overview article discussing it and circumscribing it (1879a), although this name was used by him in several binomials prior to that article (Baillon, 1879b). In his circumscription of *Uragoga*, Baillon synonymized 42 previously published generic names and thus rendered *Uragoga* an illegitimate superfluous name. Baillon circumscribed *Uragoga* very broadly, to comprise extensive morphological variation and a heterogenous group including most of the species of the Psychotrieae as well as some species now classified in other tribes. Baillon made few nomenclatural combinations in *Uragoga* for previously described species, but he did describe several new species in this genus. Petit (1964: 16) fixed the identity of *Uragoga* by selecting *U. ipecacuanha* (Brot.) Baill. as its lectotype.

Mueller (1881) studied the Psychotrieae of Brazil and some adjacent regions, and his classification differed substantially from that of previous authors (Taylor, 1996). Mueller separated Hooker's *Psychotria* into two genera, *Mapouria* Aubl., which generally corresponds to today's *Psychotria* subg. *Psychotria* (sometimes also called *Psychotria* s. str.), and "*Psychotria*," which generally corresponds to the Neotropical groups *Psychotria* subg. *Heteropsychotria* Steyerm. plus *Palicourea* (Steyermark, 1972) and to Andersson's *Palicourea* s.l. (Andersson, 2001). Mueller (1881: 163) separated *Mapouria* and *Psychotria* here based on pyrene form, in particular the presence or absence of an adaxial sulcus; however, in practice he certainly used some additional characters, because the fruits of a number of species that he classified were unknown to him. In contrast to previous taxonomists, Mueller regarded inflorescence features as widely variable within a genus, and accordingly he synonymized *Cephaelis*, *Palicourea*, and *Carapichea* and included their morphological variation all within his circumscription of *Psychotria*. (He did not study *Evea*, which was only known from outside his flora region.) The species included in *Carapichea* in its new circumscription here were classified by Mueller variously in *Mapouria* and *Psychotria*.

Schumann (1891: 119–120) followed Hooker in including species with branched inflorescences and small bracts in *Psychotria* and species with headlike or capitate inflorescences and well-developed bracts

in a separate genus. However, Schumann followed Baillon (1879a) and used the name *Uragoga* for this latter genus, though he circumscribed *Uragoga* more narrowly than Baillon did. Schumann also included several previously published names as synonyms of *Uragoga*, in particular *Cephaelis*, *Carapichea*, *Evea*, and *Callicocca*, and expanded the circumscription of *Cephaelis* to include some species with headlike inflorescences but without well-developed involucral bracts. Schumann followed Mueller (1881) in part as well and separated the species that were included in Hooker's *Psychotria* into two genera: *Mapouria*, which generally corresponds to today's *Psychotria* subg. *Psychotria*, and "*Psychotria*," which generally corresponds to *Psychotria* subg. *Heteropsychotria* minus the species with capitate inflorescences. Schumann did not present a species-level classification, but he accepted much of Mueller's classification, so the species included in the new circumscription here of *Carapichea* here were classified variously in Schumann's *Mapouria*, *Psychotria*, and *Uragoga*.

Kuntze (1891) followed Baillon's (1879a) taxonomy, recognizing a similarly broad circumscription of *Psychotria*, and used the name *Uragoga* for this group. He published hundreds of new nomenclatural combinations and replacement names for all the species of the genera that Baillon synonymized with *Uragoga*. Kuntze's classification was not adopted by subsequent authors.

In the 20th century Bremekamp studied Neotropical *Psychotria* and related genera in the Guianas, and noted that the species with headlike or capitate inflorescences and well-developed bracts that had been previously classified in *Cephaelis* comprised a heterogeneous group of species (Bremekamp, 1934: 297). Accordingly, he separated these species among several genera based on details of the arrangement and development of the inflorescence bracts: *Psychotria*, *Cephaelis*, *Petagomoa* Bremek., and *Gamotopea* Bremek. (the last two names are anagrams of *Tapogomea*, which Bremekamp cited as an older name for *Cephaelis*). Bremekamp included in *Cephaelis* only those species with flowers regularly subtended by bracts or bracteoles and rather broad, partially fused involucral bracts. He synonymized *Carapichea* here under *Cephaelis* and published the purportedly new nomenclatural combination *Cephaelis guianensis* (Aubl.) Bremek. for it; however, that combination had been previously published by Standley, making Bremekamp's name an isonym. Bremekamp synonymized two additional names with *Cephaelis guianensis*, *Cephaelis involucrata* Willd. and "*Cephaelis aubletii* DC." The name *Cephaelis involucrata* is an illegitimate name that was offered as an unnecessary substitute name for *Carapichea guianensis*; Bremekamp's name "*Cephaelis aubletii*" is apparently a typographical error for *Carapichea aubletii*.

In his various floristic surveys of Neotropical Rubiaceae, Standley (e.g., 1930, 1931a, 1931b, 1931c, 1936) separated *Cephaelis* from *Psychotria* based on details of the inflorescence features and development of the bracts. Standley did not study the plants of the Guianas in detail and did not explicitly cite *Carapichea* as a synonym of *Cephaelis* but did (Standley, 1929: 335) transfer the type species of *Carapichea* into *Cephaelis*, even though *Carapichea* is the older name. The name *Cephaelis* was conserved with respect to *Carapichea* in order to stabilize names in this group (e.g., Standley, 1916; Bremekamp, 1934); however, the name *Carapichea* is available when these genera are separated (Andersson, 2002a).

Steyermark (1972) extensively studied Neotropical *Psychotria* and related genera in northwestern South America, and presented a very different taxonomy from previous authors. Similarly to Mueller (1881) and to Petit studying *Psychotria* in Africa (1964), Steyermark regarded the branched versus headlike or capitate inflorescence structure as variable within a genus and did not separate *Cephaelis* from *Psychotria*. Similarly also to Mueller (1881), Steyermark divided the Neotropical species of *Psychotria* into two groups based on stipule morphology and pyrene morphology, which he treated as *Psychotria* subg. *Psychotria* and *Psychotria* subg. *Heteropsychotria*; however, he also separated *Palicourea*, which Mueller combined with the species of Steyermark's *Psychotria* subg. *Heteropsychotria*.[1]

[1] The differences between his two subgenera of *Psychotria* were presented in formal diagnoses (Steyermark, 1972: 444, 484), which distinguished them by stipule and pyrene features. In this work Steyermark also presented a key to individual species, in the course of which he keyed, or partially keyed, some of the infrageneric taxa. Several species from each subgenus are keyed in the first part of this, without mention of subgenera; then the remaining, less distinctive species are separated into subgenera in couplet #218 (of 405 couplets). Among these species the subgenera are separated by stipule features and drying color of the plants, and this has sometimes been considered Steyermark's functional separation of these two subgenera. These characters generally can be used to separate them in most cases. However, this lead keys less than half of the *Psychotria* species classified in this work, because the characters in couplet #218 do not key some of the species to subgenus, and Steyermark's formal diagnosis of the characters of *Psychotria* subg. *Heteropsychotria* does not include drying color. It may be that Steyermark intended couplet #218 of this key to diagnose the subgenera, and he did not in fact consider the pyrene characters meaningful (Kirkbride, pers. comm.), but that is not evident from internal evidence in this publication.

Steyermark synonymized several genera under *Psychotria* subg. *Heteropsychotria*, including *Cephaelis* (1972: 484), *Uragoga* (1972: 484), and *Carapichea* (1972: 676, this specifically listed under *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg.). As noted by Andersson (2002b) and Taylor (1996), Steyermark's *Psychotria* subg. *Psychotria* corresponded to pantropical *Psychotria* as circumscribed by Petit (1964), whereas the entirely Neotropical *Psychotria* subg. *Heteropsychotria* included the rest of the Neotropical species that were previously classified in *Psychotria* plus *Cephaelis* by Hooker (1873) and in *Psychotria* plus *Uragoga* by Schumann (1891). Steyermark's *Psychotria* subg. *Heteropsychotria* generally corresponds to Mueller's circumscription of *Psychotria* minus the species Steyermark separated in *Palicourea*. Thus, *Psychotria* subg. *Heteropsychotria* is morphologically very diverse (Taylor, 1996), and molecular studies have since shown that it comprises a systematically heterogeneous group of species (Andersson & Rova, 1999; Nepokroeff et al., 1999; Andersson, 2002b). As detailed in the individual discussions of the informal species groups presented here, the species that are included in the new circumscription of *Carapichea* here were variously classified by Steyermark in different sections and series of *Psychotria* subg. *Heteropsychotria*: *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg. (Steyermark, 1972: 676), *Psychotria* sect. *Notopleura* Oerst. ser. *Altsonii* Steyerm. (1972: 555), *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm. (1972: 484), and the unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574) and its unnamed and undiagnosed *Psychotria* ser. A (1972: 574) and *Psychotria* ser. C (1972: 588).

In his study of African *Psychotria*, Petit (1964) distinguished genera based primarily on pyrene and seed characters, in particular the presence and arrangement of preformed germination slits (PGSs) and the presence or absence of alcohol-soluble pigments in the seed coat. Pyrene morphology well characterizes *Psychotria* subg. *Psychotria* but is now known to be variable among the species included in *Psychotria* subg. *Heteropsychotria* (Piesschaert, 2001), and it is far from thoroughly reviewed or understood in this group. Some species and species groups are consistently characterized by pyrene morphology, but variation in pyrene characters within species groups and even within individual species has been documented as well (Piesschaert et al., 1998; Piesschaert, 2001). Steyermark discussed Petit's work and pyrene characters in his Neotropical *Psychotria* studies, but he did not document these extensively for the species he studied and did not really incorporate them into his classification. For example, several of the pyrene features that he said characterized some groups (e.g., *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm.) are not actually found in all the species he included in those groups (Piesschaert, 2001). In practice, Steyermark's classification was based on other characters as well, apparently in particular stipule form, drying color of the specimens, and various details of the inflorescence arrangement.

Nepokroeff et al. (1999), Andersson and Rova (1999), and Andersson (2002a, 2002b) studied *Psychotria* and related genera using molecular sequence data and found two distinct clades, one including *Psychotria* subg. *Psychotria*. and the other comprising several genera including *Palicourea*, *Geophila* D. Don, *Chassalia* Comm. ex Poir., and *Rudgea* Salisb. This second clade has been variously called the *Palicourea* complex (Andersson, 2002a) or the *Palicourea* group (Andersson, 2001), and corresponds generally to the Palicoureeae of Robbrecht and Manen (2006) and Razafimandimbison et al. (2008). These studies also found that most of the Neotropical species included in *Psychotria* subg. *Heteropsychotria* are more closely related to *Palicourea* than to *Psychotria*. Andersson (2001) treated the species of *Psychotria* subg. *Heteropsychotria* plus *Palicourea* as a combined group he called *Palicourea* s.l.; however, he excluded several species from *Psychotria* subg. *Heteropsychotria* that were placed on a sister clade to *Palicourea* s.l. in the molecular analyses. *Palicourea* s.l. includes at least 600 species that currently have names variously in *Palicourea* and *Psychotria* and in many cases are very poorly known, and it has no comprehensive infrageneric classification; these genera are currently being combined and an infrageneric classification outlined bit by bit as the species are studied (e.g., Taylor et al., 2010).

In their molecular analysis, Nepokroeff et al. (1999) studied one species now included in *Carapichea*, *Psychotria ipecacuanha* (Brot.) Stokes (= *Carapichea ipecacuanha*), and found this species to be placed in the large clade that included *Palicourea* together with *Geophila* and *Chassalia*, but in a separate subclade from *Palicourea*. They called this subclade Other Psychotrieae. Andersson (2001) studied a different species that is now included in *Carapichea*, *Psychotria ligularis* (Rudge) Steyerm., and found that species included in his *Palicourea* group. The identity of the plant Andersson studied as *Psychotria ligularis* was subsequently clarified: the specimen identified as *Psychotria ligularis* in those studies (e.g., Andersson, 2001, 2002b) is the same collection, *Andersson et al. 1989* (MO!), that was later

re-identified as *Carapichea guianensis* (Andersson, 2002a: 364). As clarified by Delprete (2001, 2003), *C. guianensis* and *C. ligularis* are two different species, and this particular voucher specimen belongs to *C. guianensis*. (These two species were synonymized by Steyermark [1972] so the identifications used by Andersson all followed current taxonomy of the time.)

Andersson (2002a) used these results to focus on the relationships of several species of the *Palicourea* group in more detail and found *Psychotria ipecacuanha* (= *Carapichea ipecacuanha*) placed in a well-supported clade together with *Psychotria borucana* (Ant. Molina) C. M. Taylor & W. C. Burger (= *C. affinis*) and *Psychotria guianensis* (= *C. guianensis*). Accordingly, he placed these three species into a separate genus, for which he revived the name *Carapichea* based on the inclusion of its type species, *C. guianensis*. Andersson presented a morphological characterization and diagnosis of *Carapichea* but left the full species circumscription and further morphological detailing of this genus for the future. Instead of presenting a complete diagnosis of *Carapichea*, he outlined the morphological characters that separate it by distinguishing the related genera. He distinguished *Chassalia*, *Geophila*, *Margaritopsis*, *Notopleura*, and *Rudgea* from *Carapichea* by their different arrangements of the PGSs of the pyrenes and separated *Hymenocoleus* Robbr. from *Carapichea* by its ochrea-like structures on the stem nodes inside the stipules, which are lacking in *Carapichea* (Andersson, 2002a: 370) and in fact unique in the Rubiaceae. He also separated *Carapichea* from *Psychotria* subg. *Psychotria* by its "non-caducous stipules, pyrenes with distinct germination slits on abaxial ridges (rather than marginally) and testa without ethanol-soluble pigment," and a lack of ant domatia (2002a: 370) in contrast to caducous stipules, pyrenes with marginal PGSs, and seed testa with an ethanol-soluble red-brown pigment, along with the ant domatia found in a very few species of *Psychotria*. However, the characters that he cited to separate *Carapichea* from *Psychotria* are all found in *Palicourea*, so Andersson (2002a: 370) then separated these last two genera: "*Carapichea* differs from *Palicourea* s. l. in having aperturate pollen, and furthermore . . . in not having bipartite stipule lobes and in having the adaxial pyrene furrow with irregular (rather than smooth) margins, in contrast to inaperturate pollen, bipartite stipules, and pyrenes with an adaxial furrow with entire or smooth margins in *Palicourea*."

Delprete (2001) studied *Psychotria ligularis* as circumscribed by Steyermark (1972) and concluded that it comprised two distinct species, *P. ligularis* and *P. carapichea* (Steyerm.) Delprete. Shortly afterward Delprete followed Andersson in recognizing *Carapichea* (Boom & Delprete, 2002; Delprete, 2003), clarified that *P. carapichea* is correctly called *C. guianensis* (Delprete, 2003), and added a fourth species to the genus, *C. ligularis* (Delprete, 2003).

Jardim and Zappi (2008) subsequently described an additional species, *Carapichea lucida* J. G. Jardim & Zappi from eastern Brazil, and rather significantly emended Andersson's morphological characterization of this genus. They stated that *C. lucida* "is well placed within the genus *Carapichea* based on its marcescent stipules, its fruit colour, which is purple and dyes alcohol with a deep purple tinge, the presence of one basal-ventral pregermination slit [i.e., the pyrene with one basal-adaxial PGS], and its glomerulate inflorescence protected by green bracts." The marcescent stipules they cited agree with the general morphological characterization of *Carapichea* by Andersson (2002a), although this character was not noted by him to diagnose the genus and also characterizes some other genera of Psychotrieae (e.g., *Margaritopsis*; Taylor, 2005). Their characterization of *Carapichea* as having a "basal-ventral" germinal slit on the adaxial face of pyrene differs markedly from Andersson's description of PGSs located along the ribs of the abaxial surface of the pyrene. Fruit color and fruit pigments were not cited as diagnostic for *Carapichea* by any previous authors; Andersson (2002a: 371) characterized the genus as having variously "orange, red, blue, purplish, or blackish" fruits. Andersson also characterized the inflorescences of *Carapichea* as "congested and involucrate" (2002a: 371), but he did not mention the bract color nor did he include the inflorescence arrangement in a list of diagnostic features.

In a broad analysis of available molecular systematic data in Rubiaceae, Robbrecht and Manen (2006) also found *Carapichea* to be much more closely related to *Palicourea* than to *Psychotria*, and they included it in their newly described tribe Palicoureeae. In a study of the Psychotrieae and closely related tribes, Razafimandimbison et al. (2008) also found the Palicoureeae well supported by molecular data; however, their analysis did not include *Carapichea*. In a broad molecular analysis of all of Rubiaceae with more taxon sampling than previous works (Bremer & Eriksson, 2009), the species of *Carapichea* that were studied (*C. ipecacuanha* and *C. affinis*, identified there as *Psychotria ipecacuanha* and *P. borucana*) were placed on a large clade that included *Palicourea* and several other genera and within this on a separate subclade from *Palicourea* together with *Geophila* plus one species of

Chassalia (*C. parviflora* Benth.); the other species of *Chassalia* were placed on a different clade. Bremer and Eriksson did not separate Palicoureeae from Psychotrieae here, noting that their classification was conservative, and they found the support here for two tribes very weak.

Characterization and Circumscription of *Carapichea*

Andersson (2002a) presented a morphological characterization of *Carapichea* based on both the characters it possesses and the characters that are found in other genera but lacking in *Carapichea* based on study of three species that were incompletely known. Andersson separated *Carapichea* based on, overall, the presence of PGSs located along the abaxial ridges of the pyrenes, "non-caducous stipules," aperturate pollen, and adaxial pyrene furrows with irregular margins, along with the lack of ochrea-like structures on the stem nodes, ethanol-soluble pigments in the testa, and bipartite stipule lobes. Jardim and Zappi (2008) later considered *Carapichea* to be additionally diagnosed by the presence of marcescent stipules, glomerulate inflorescences enclosed by green involucral bracts, purple fruit with an alcohol-soluble purple pigment, and pyrenes with a single basal-adaxial PGS. The stipule form, fruit color, and inflorescence characters cited by Jardim and Zappi do not conflict with the species included in *Carapichea* by Andersson, except the inflorescence bracts of *C. affinis* are often purple rather than green. However, the form of the pyrene PGSs they describe does conflict with that noted by Andersson, which shows that either *C. lucida* is incorrectly classified or Andersson's morphological characterization of *Carapichea* merits some review now that more specimens are available. Accordingly several of Andersson's characters, the pollen, stipules, and pyrenes, are re-evaluated here; the ochrea-like stem structures and ethanol-soluble pyrene pigments are absent from *Carapichea* as circumscribed here.

Andersson (2002a) studied the pollen of two *Carapichea* species, *C. affinis* and *C. ipecacuanha*, but did not have flowers of *C. guianensis* available. He found the pollen to be aperturate and noted that in contrast the species of *Palicourea* s.l. studied all have inaperturate pollen. Andersson's characterization of the pollen of *Palicourea* cited Johansson's (1992) study of 12 species that molecular analyses showed belong to *Palicourea* s.l. Additionally, based on morphological characterization (Taylor, 1996), nearly all of the ca. 50 species that were included in Johansson's Neotropical group XXI and group XXII, both with inaperturate pollen, belong to *Palicourea* s.l.; however, an exception here is *Psychotria patria* Standl. & Steyerm. of group XXI, which is now included in *Notopleura patria* (Standl. & Steyerm.) C. M. Taylor (Taylor, 2001a). Andersson (2002a: 36) himself noted in his characterization of *Carapichea* that inaperturate pollen is a "homoplasious synapomorphy" found in some individual species belonging to various genera of Psychotrieae that generally have aperturate pollen (e.g., *Rudgea*, *Hymenocoleus*, *Chassalia*). Thus, aperturate pollen does characterize *Carapichea*, but future discovery of inaperturate pollen in the genus is not precluded.

"Bipartite stipule lobes" (Andersson, 2002a: 370), also called bifid stipules (Andersson, 2002a: 369) or bilobed stipules (Taylor, 1996), is the most common stipule form in Psychotrieae. This has been cited as characteristic of several genera, but both interpetiolarly entire and interpetiolarly bifid stipules are found in many Psychotrieae genera (e.g., *Notopleura*, *Margaritopsis*, *Chassalia*). Thus, variation may be expected in stipule form within *Carapichea* as well, and in fact the three species included in *Carapichea* by Andersson vary widely in this: *C. ipecacuanha* has multi-lobed or fimbriate stipules; *C. affinis* has ovate entire stipules; and *C. guianensis* has stipules that range from entire to minutely bilobed, entire then tardily splitting into two segments, or initially bilobed for up to half their length (e.g., *Feuillet & André 1405*, MO!). This variation in stipule form in *C. guianensis* has not been noted in the very few published descriptions of this species (e.g., Boom & Delprete, 2002), but is apparent when specimens are studied in detail. Thus, the stipule form cited by Andersson does not diagnose *Carapichea*.

As noted by Petit (1964) and Piesschaert (2001), some pyrene characters are diagnostic for some genera of Psychotrieae, in particular the presence and arrangement of PGSs and the presence of ethanol-soluble pigments in the testa. Andersson (2002a) studied pyrene morphology of *Carapichea guianensis* and *C. affinis*, but did not have fruits available of *C. ipecacuanha*. The pyrenes of the two species he studied lack ethanol-soluble pigments and have the PGSs located along the abaxial ridges. Andersson characterized *Carapichea* by the arrangement of the PGSs and the form of the adaxial pyrene furrow or groove, in particular by its well-developed irregular margins. These pyrenes are similar in the PGS arrangement and the deep adaxial furrow to species of *Palicourea* s.l., where Piesschaert (2001: 309) found apparently similar furrow margins in several species (e.g., *Palicourea pittieri* Standl., *Psychotria capitata* Ruiz & Pav.) and some other genera (e.g., *Chassalia*, Piesschaert et al., 2001). He also documented

variation in the furrow margins from rudimentary to well developed, even within some individual species such as *C. ligularis* (Piesschaert, 2001: 280, as *Psychotria ligularis*). In addition, none of Andersson's characteristic features of *Carapichea* are found in the pyrenes of *C. ipecacuanha*, for which fruits are now available. These pyrenes have a weak line or ridge instead of a furrow on the adaxial surface (Fig. 1A–C) and dehisce along the adaxial face through a basal pore and a short medial slit. Thus, the arrangement of their PGSs is similar to that of *C. lucida*. The pyrenes of *C. ipecacuanha* are also longitudinally twisted, a form previously known only in *Geophila* (Piesschaert et al., 1998). Thus, the pyrene characters cited by Andersson do not completely separate *Carapichea* from other genera, and the PGS arrangement of *C. lucida* is not unique in the genus.

The species that have been included in *Carapichea* do share several other distinctive morphological features that apparently diagnose this genus and identify additional species for inclusion in *Carapichea*. The characters that are here considered together to diagnose *Carapichea* are: a characteristic marcescent stipule form, inflorescences that are capitate or branched to one to two orders with the flowers sessile to shortly pedicellate, lack of ethanol-soluble pigments in the testa, and aperturate pollen of a generalized form. Based on these characters, 18 additional species are here transferred to *Carapichea*, which expands the morphological features found in this genus as discussed in more detail in the next section. In particular, there is rather extensive variation in stipule shape, inflorescence form, and the arrangement of the preformed germination slits of the pyrenes. Although *C. lucida* is quite distinctive, it agrees with the morphological characters found in this genus and appears to be correctly classified. Additionally, recent phytochemical analyses indicate that *Carapichea* also differs markedly in the chemistry of its alkaloids from *Psychotria* subg. *Heteropsychotria* and *Psychotria* subg. *Psychotria* (Bernhard et al., 2011), but taxonomic sampling in those analyses is still very limited. All the molecular studies of the tribe Psychotrieae have found very complex systematic patterns that are not yet well understood, both in the tribe and within the species-rich genera, so the expanded delimitation and morphological characterization of *Carapichea* presented here provide a detailed hypothesis that can now be tested further.

The relationships of *Stachyococcus* Standl. within the tribe Psychotrieae have been unclear (Taylor, 1996), but it has the characters of *Carapichea* as circumscribed here, in particular the stipule features, its flowers sessile in headlike glomerules borne in unbranched inflorescences, its relatively large fruits for *Palicourea* s.l., and the general similarity of its leaf venation to some other species of *Carapichea*, such as *C. klugii* (Standl.) C. M. Taylor. Accordingly, this species is here included in *Carapichea*.

The relationships of the species of *Psychotria* ser. *Altsonii* have also been unclear. Steyermark (1972: 555) grouped these four poorly known species together based on the arrangement of the inflorescence bracts and the supposedly sheathing truncate stipules and considered them related to *Notopleura*. Taylor et al. (2004) also considered these species related to *Notopleura* based on their habit, stipule form, leaf characters, and inflorescence arrangement. However, more detailed study shows that these all differ from *Notopleura* in their consistently terminal inflorescences and interpetiolar rather than sheathing stipules that lack glandular appendages. These four species are provisionally grouped together here based on Steyermark's observations and are included in *Carapichea* based on their inflorescence arrangement and stipules. Their stipules are interpetiolar and become marcescent with age, then fall off through fragmentation, leaving a markedly thickened scar (*C. altsonii* (Sandwith) C. M. Taylor) or hardened persistent basal portion (the three other species).

The species of *Carapichea* are arranged here in informal groups, which are partly characterized by one or a few morphological features. The separation of these groups aids identification of the species and highlights the morphological variation in this genus. The features that characterize these species groups may also indicate relationships, but many of the species are very poorly known. *Carapichea* itself is not well understood; these groups are therefore provisional and not formally named here.

Morphological Survey of the Species of *Carapichea*

A number of morphological features vary within *Carapichea*, including details of the stipule shape, degree of inflorescence branching, arrangement and development of the inflorescence bracts, corolla size and color, pollen form, fruit size and color and form and dehiscence mode of the pyrenes. However, these same features also vary within related genera (e.g., *Notopleura*, Taylor, 2001a; *Palicourea*, Taylor, 1997a), so this variation is not necessarily exceptional within *Carapichea*.

VEGETATIVE MORPHOLOGY

The dried specimens of many *Carapichea* species share a distinctive grayish green, grayish brown,

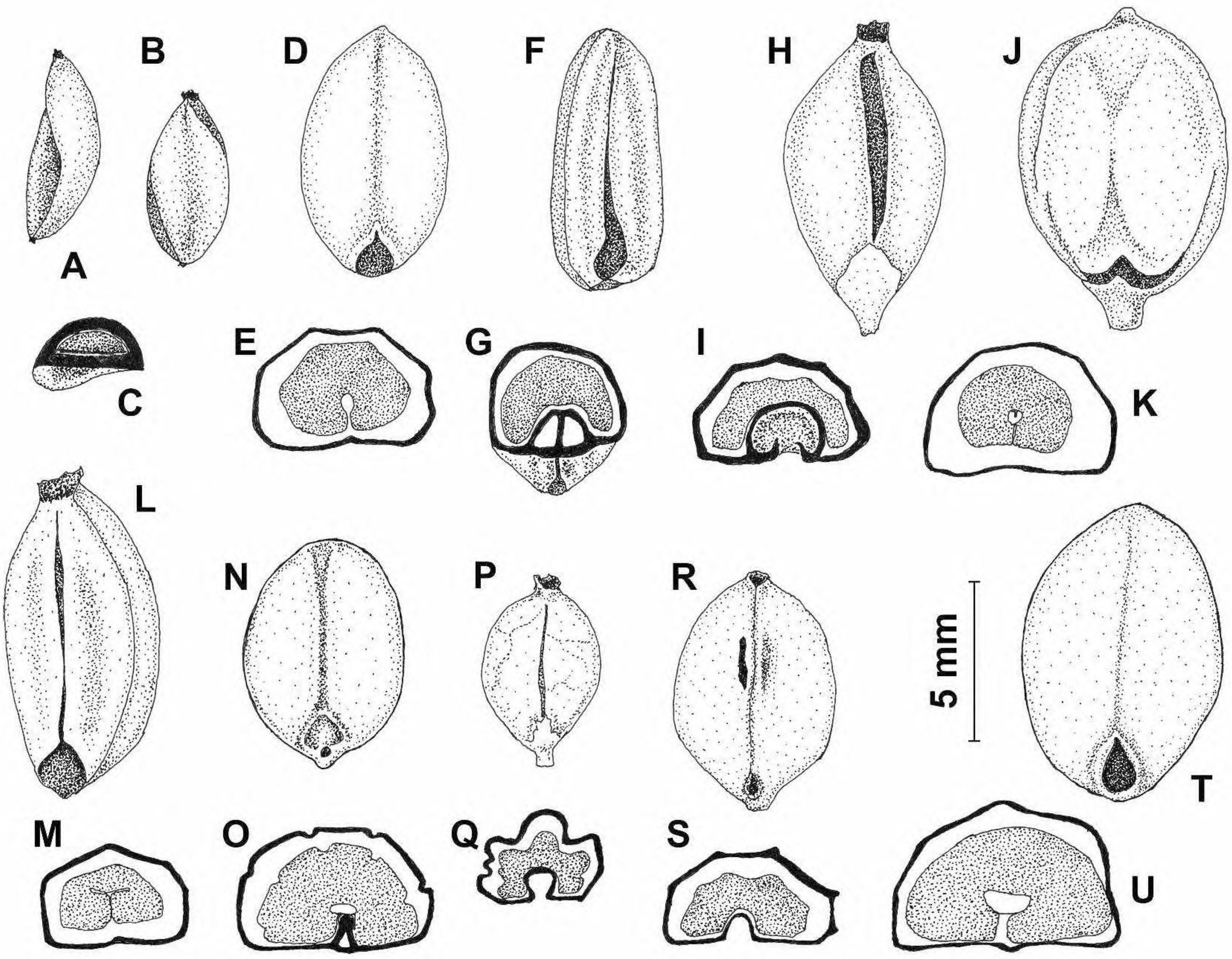


Figure 1. Pyrenes of selected *Carapichea* species, each with a view of the adaxial (i.e., ventral) face and a schematic cross-section near middle. Species order follows the text. All figures to same scale. In the schematic cross-sections, pyrene walls are in black and endosperm is stippled; these drawings are based on dried specimens, with endosperm sometimes shrunken. A–C. *Carapichea ipecacuanha* (Brot.) L. Andersson (*Ipecacuanha* group), based on *L. A. Skorupa et al. 712* (MO). —A. Pyrene side view. —B. Pyrene adaxial view. —C. Cross-section of pyrene. D, E. *Carapichea affinis* (Standl.) L. Andersson (*Carapichea* group), based on *E. Rodríguez et al. 1160* (MO). —D. Pyrene adaxial view. —E. Schematic cross-section of pyrene. F, G. *Carapichea guianensis* Aubl. (*Carapichea* group), based on *P. Acevedo et al. 5924* (MO). —F. Pyrene adaxial view. —G. Cross-section of pyrene, showing air chambers formed by pyrene wall. H, I. *Carapichea maturacensis* (Steyerm.) C. M. Taylor (*Carapichea* group), based on *B. Stein & A. Gentry 1698* (MO). —H. Pyrene adaxial view, with raphal plug still attached. —I. Cross-section of pyrene showing concave intrusion with extended margins of pyrene wall. J, K. *Carapichea ligularis* (Rudge) Delprete (*Pacimonica* group), based on *L. Andersson 1989* (MO). —J. Pyrene adaxial face. —K. Schematic cross-section of pyrene. L, M. *Carapichea pacimonica* (Müll. Arg.) C. M. Taylor (*Pacimonica* group), based on *B. Stergios et al. 16280* (MO). —L. Oblique view of adaxial pyrene face. —M. Schematic cross-section of pyrene. N, O. *Carapichea urniformis* (Steyerm.) C. M. Taylor (*Altsonii* group), based on *D. Clarke et al. 8963* (MO). —N. Pyrene adaxial face. —O. Schematic cross-section of pyrene. P, Q. *Carapichea panurensis* (Müll. Arg.) C. M. Taylor (*Panurensis* group), based on *L. Kawasaki 204* (MO). —P. Pyrene adaxial face, with raphal plug still attached. —Q. Schematic cross-section. R, S. *Carapichea tillettii* (Steyerm.) C. M. Taylor (*Panurensis* group), based on *D. Clarke et al. 10713* (MO). —R. Pyrene adaxial face. —S. Schematic cross-section of pyrene. T, U. *Carapichea adinantha* (Standl.) C. M. Taylor (*Stachyococcus* group), based on *R. Vásquez et al. 2192* (MO). —T. Pyrene adaxial face. —U. Schematic cross-section of pyrene.

yellowish brown, brown, or greenish brown color, which may be related to the chemistry of these species, but specifics of this are unknown. Drying color varies within some Rubiaceae genera (e.g., *Gaertnera* Lam.; Malcomber & Taylor, 2009), but is rather consistent and sometimes distinctive in others (e.g., *Psychotria* subg. *Psychotria*; Hamilton, 1989). The gray or blackened color found in many species of *Carapichea* is similar to that found in several species of *Psychotria* subg. *Psychotria* (e.g., *P. marginata* Sw.), but these genera are not very similar chemically (Bernhard et al., 2011).

The morphology of the stipules is useful for diagnosing and distinguishing many Psychotrieae genera (Taylor, 1996, 2005) and appears to be a diagnostic feature for *Carapichea*. The stipules of the species included here in *Carapichea* are interpetiolar, apparently lack glands on the margins and external

(i.e., abaxial) surface, and are marcescent or deciduous in a characteristic way: the margins become brown and dry, then the stipule body becomes a little indurated and sometimes also yellowed, then the stipule breaks up via fragmentation with age. These indurated fragmenting stipules are similar to those of *Margaritopsis*; however, the stipules of *Margaritopsis* are generally also glandular on the tips of the lobes and/or along the margins. *Carapichea*'s hardening and fragmenting stipules differ from those of most species of *Palicourea* s.l., although the stipules of a few species are similar in this regard (e.g., *P. palustris* A. C. Gilman & C. M. Taylor; Gilman & Taylor, 2008). In form, the stipules of *Carapichea* vary among the species from entire to deeply bilobed, and this entire range of variation is also found within a few species (e.g., *C. guianensis*). The laciniate stipules of *C. ipecacuanha* are unique within *Carapichea* although this stipule form is found in some related genera (e.g., *Rudgea*; Taylor et al., 2004).

Some details of the leaf venation vary markedly within *Carapichea*, but several of the informal species groups recognized here are characterized in part by distinctive venation arrangements. In most species of *Carapichea* the leaf venation is similar to that found widely in the Psychotrieae, with well-developed eucamptodromous or brochidodromous secondary veins, few and short but regularly developed intersecondary veins, and evident reticulated tertiary venation. However, in several *Carapichea* species the intersecondary veins are numerous and exceptionally well developed (*Pacimonica* group), while in some other species the venation is hardly evident (*Panurensis* group) or not at all visible (*Altsonii* group). No tuft or crypt domatia (Robbrecht, 1988) have been seen, although the species of the *Pacimonica* group have a line of short pubescence extending along each side of the midrib on the lower leaf surface that may have a function similar to the axillary domatia.

INFLORESCENCES AND FLOWERS

Inflorescence form is markedly variable within many genera of Rubiaceae (e.g., Petit, 1964; Steyermark, 1972; Taylor, 2001a; Malcomber & Taylor, 2009), but sometimes general characteristics are shared within a genus. The species included here in *Carapichea* share inflorescences with sessile or very shortly pedicellate flowers arranged in small to large groups, with the flowers or flower groups borne terminally on the inflorescence axes when these are developed. However, inflorescence arrangement varies widely from a single, sometimes involucrate, very compactly branched headlike (i.e., "capitate") or almost headlike (i.e., "subcapitate") structure with the floral bracts lacking to well developed, to a thyrse that is branched to several orders, with the bracts varying from developed to reduced. The inflorescence form of some *Carapichea* species changes over time: the inflorescence is typically capitate or subcapitate when the first flowers open, but becomes laxly branched to one or even two orders by the time the last fruits are maturing (e.g., *C. ligularis*, *C. tillettii* (Steyerm.) C. M. Taylor). In flower and fruit the inflorescence axes and bracts may range from green to white, or be bright pink or purple. In several species the flowers are immediately subtended by a distinctive ring of pilose or sericeous pubescence (e.g., species of the *Pacimonica* group); as noted by Steyermark (1972), similar pubescence is also found in some species of *Palicourea* s.l. (e.g., *Psychotria trichocephala* Poepp. & Endl.).

The corollas of *Carapichea* are most commonly short (4–8 mm long), white, and presumably pollinated by bees or other insects (e.g., *C. ipecacuanha*) but also vary in size (to 12–15 mm long), are variously yellow, orange, pink, or purple in color, and are pollinated apparently by butterflies or hummingbirds (e.g., *C. pacimonica* (Müll. Arg.) C. M. Taylor). The flowers of at least some species are distylous, but many species of *Carapichea* are so poorly documented that their floral biology cannot be determined.

Johansson (1992) detailed the pollen morphology of several of the species newly included here in *Carapichea* (as species of *Psychotria*) and found it to be aperturate in all of them. Johansson placed these species in two of his pollen morphological groups, group XIV with 3- to 5-colpate grains, which comprised only *C. vasivensis* (Müll. Arg.) C. M. Taylor, and group XVI, with 3- to 5-colpate, -porate, or -colporate grains, comprising *C. pacimonica*, *C. tillettii*, and about 45 other Neotropical and African species. Johansson noted that the pollen of his group XVI was variable in several features, and this particular group included species that are not all closely related and have a rather generalized pollen form; the other species of Johansson's group XVI are today classified in *Margaritopsis*, *Notopleura*, *Palicourea* s.l., *Rudgea*, *Psychotria* subg. *Psychotria*, and the tribe Lasiantheae (*Ronabea*).

FRUITS AND PYRENES

The fruits of the species included here in *Carapichea* vary from orange, red, dark red, blue, or dark purple to black, although in some species the fruits apparently pass through a red or orange immature phase and ultimately turn dark-colored or

black when ripe (e.g., *C. araguariensis* (Steyerm.) C. M. Taylor), and *C. verrucosa* reportedly has white or yellow fruits. Andersson (2002a) noted that the pyrenes of the two *Carapichea* species he studied are larger than average in his *Palicourea* group, but the species now included here have a wide range of pyrene sizes. Relatively large pyrenes are necessarily borne in relatively large fruits, so pyrene size may be correlated more with fruit dispersal of individual species than a genus-level feature.

The pyrenes of most of the species included here in *Carapichea* have a planoconvex shape, several low ribs or ridges on the abaxial (i.e., dorsal) side, and a weak to well-developed longitudinal central furrow on the adaxial (i.e., ventral) side (Fig. 1). This adaxial furrow corresponds to an adaxial invagination in the seed, similar to the general form found in *Palicourea* s.l. (Piesschaert, 2001), although in *Carapichea* species this furrow is more often widened at the base. The PGSs are positioned along the abaxial ridges, adaxially along the basal portion of the adaxial furrow, around the basal or raphal (Robbrecht, 1988) plug, or sometimes along the basal portions of the margins. Pyrene features in part characterize several of the informal species groups presented here.

The pyrenes of *Carapichea ipecacuanha*, the only species of the *Ipecacuanha* group, differ from those of other species of *Carapichea*. These are planoconvex, abaxially smooth except with one low, sharp, median ridge, adaxially flat or with a slender longitudinal thickening, and longitudinally twisted (Brazil, *L. A. Skorupa et al. 712*, MO!; Panama, *Croat 12427*, MO!, *Busey & Croat 237*, MO!; Fig. 1A–C). The twisting is gentle but clearly evident in all pyrenes seen. The adaxial ridge is weakly developed and arises from a basal thickening or plug and extends through the basal half of the pyrene. Dehiscence is via splitting along the sides of the basal plug plus a longitudinal slit that extends along the basal half of the adaxial face. These pyrenes are similar in form and dehiscence to the pyrenes of some species of *Geophila* (Piesschaert et al., 1999). The dehiscence of these pyrenes is similar to that found in the *Stachyoccoccus* group and the Bahia group, but their longitudinal twist is unique within *Carapichea*.

The pyrenes of the *Carapichea* group were first studied by Andersson (2002a, *C. guianensis*) and Piesschaert (2001: 280; *C. ligularis*, as *Psychotria ligularis*). These are notable in having a well-developed broad adaxial furrow that extends for the entire length of the pyrene and is relatively deep, generally occupying a fourth to half of the pyrene. This adaxial furrow is, however, mostly enclosed by thin, usually irregular extensions of the pyrene wall, as described in detail by Andersson (2002a). These pyrenes are similar in this well-developed adaxial furrow and its thin, irregular margins to pyrenes of some species of *Chassalia* studied by Piesschaert et al. (2001), with the open type pyrene form described there. On some pyrenes of *Carapichea guianensis*, the thin broad margins of the adaxial furrow extend to meet in the middle and then fold upward (i.e., abaxially), and at times even connect with the base of the furrow to form two cylindrical longitudinal air spaces (e.g., *C. guianensis*, Fig. 1F–G). However, the pyrenes of some other species of this same group have a shallow open adaxial furrow and well-developed basal plug (e.g., *C. affinis*, Fig. 1D–E). In these species dehiscence is through the basal or raphal aperture that is formed when the enlarged tissue plug falls away plus a slit that extends along the adaxial furrow and sometimes also along short slits on the basal portions of the margins.

In the species of the *Pacimonica* group, the pyrenes are generally similar to those of the *Carapichea* group. In particular, the pyrenes of *C. maturacensis* (Steyerm.) C. M. Taylor (Fig. 1H, I) resemble those of *C. guianensis* except the extensions of the adaxial pyrene wall cover only the furrow or are fused to create a single cylindrical air chamber (Fig. 1H, I). The pyrenes of *C. pacimonica* are similar but with only a shallow adaxial invagination (Fig. 1L, M). Piesschaert, however, described the pyrenes of *C. klugii* as adaxially concave with one median crest and two shallow grooves, which are visible on his drawing of the adaxial face of the pyrene but not in his figure D in the accompanying cross-section illustration (Piesschaert, 2001: 280, 304, fig. 8.18; as *Psychotria klugii* Standl.). These two shallow adaxial grooves apparently correspond to sculpturing around the basal plug, and Piesschaert found the pyrenes of *C. klugii* to be dehiscent variously via abaxial slits or through two marginal slits plus one abaxial slit. The pyrenes of *C. ligularis* (Fig. 1J, K) are similar to the ones Piesschaert described for *C. klugii* with dehiscence through a basal plug plus two slits along the basal parts of the margins.

The pyrenes of *Carapichea urniformis* (Steyerm.) C. M. Taylor, of the *Altsonii* group, abaxially have three or four weak angles or low longitudinal ridges and adaxially have a well-developed longitudinal central furrow that extends for the entire length of the adaxial face (Steyermark, 1972: 557, fig. 74e; as *Psychotria urniformis* Steyerm.), with a raphal plug at the basal end (Fig. 1N, O). As in the pyrenes of *C. guianensis*, this adaxial furrow is at least sometimes closed off by its thin extended margins to form a separate chamber. The mode of dehiscence of this species has not been

determined in this present study, but Piesschaert described the pyrenes of *C. urniformis* (Piesschaert, 2001: 284; as *P. urniformis*) as having "3 indistinct rounded ribs" adaxially and a "deep median groove, [and a] small endocarpal thickening above raphal opening" abaxially with the dehiscence along the abaxial ribs, although the raphal opening may also function in pyrene dehiscence. The pyrenes of the other three species of the *Altsonii* group have not been seen for this study. Piesschaert described the pyrenes of *C. altsonii* (2001: 276; as *P. altsonii* Sandwith) as having "one vague median rib" abaxially and a "conspicuous, broad median crest" adaxially, but he did not determine dehiscence mode.

The pyrenes of the *Panurensis* group are relatively small within *Carapichea* and are abaxially ridged or ribbed with a well-developed central adaxial furrow (Fig. 1P, S). They have a basal pore that is covered with a plug and sometimes also an apical pore, and dehiscence appears to be through these pores.

The pyrenes of the *Stachyococcus* group are relatively large within *Carapichea* and are dehiscent via a central adaxial furrow, a pore with a basal or raphal plug, and sometimes short basal marginal slits (Figs. 1T, U, 2C). These are similar in their PGS arrangement to the species of the Bahia group and the *Ipecacuanha* group. The pyrenes of the *Stachyococcus* group lack abaxial ridges, although the pyrenes of *C. verrucosa* are unique in *Carapichea* in their abaxial surface with verrucose ornamentation (Fig. 2C).

DISTRIBUTION AND HABITAT

Carapichea is so far only known from the Neotropics, but the worldwide Psychotrieae are not well known in many tropical regions, in particular southeastern Asia, so this genus may yet be found elsewhere. In particular, *Cephaelis stipulacea* Blume of southeastern Asia shares several characters with *Carapichea*, namely similar marcescent stipules, inflorescences with the flowers grouped into several heads that are enclosed by well-developed bracts, and relatively large pyrenes similar to those of *Carapichea guianensis* and *C. ligularis*. This species was included in *Chassalia* primarily based on its pyrene morphology by Piesschaert et al. (2001) as *Chassalia stipulacea* (Blume) Piesschaert; however, further study may show that this species is more closely related to *Carapichea*.

The majority of the species of *Carapichea* are found in the Guayana Region of northeastern South America (Berry et al., 1995) and the Amazon basin. One species, *C. lucida*, has a disjunct distribution from the rest of the genus in eastern Brazil. Several species are known mainly or only from the western Amazon basin: *C. klugii*, *C. affinis*, *C. adinantha* (Standl.) C. M. Taylor, and *C. dolichophylla* (Standl.) C. M. Taylor. Only *C. affinis* and *C. ipecacuanha* reach Central America, the former ranging to southern Costa Rica and the latter to Nicaragua.

Species of *Carapichea* are largely found at low elevations, generally 0–500 m, with only *C. affinis* ranging into premontane and lower montane vegetation (Holdridge, 1967), up to 1570 m in Ecuador and Peru. Habitat information is limited for many species, but several have been collected primarily on nutrient-poor sandy soils (*C. panurensis* (Müll. Arg.) C. M. Taylor, *C. maturacensis*), and at least one species has been collected primarily in seasonally inundated areas along nutrient-poor blackwater rivers (*C. vasivensis*). Some species are documented as widespread in noninundated sites with generalized soil types (e.g., *C. affinis*, *C. guianensis*). The mostly widely distributed species ecologically seems to be *C. klugii*, which has been collected in a variety of nutrient-poor to nutrient-rich, inundated to upland habitats.

METHODS

TAXONOMY

This work is based on study of herbarium specimens using standard techniques. Morphological terms follow Lawrence (1951). Specimens were studied from the collections of BR, COAH, F, G, MO, and NY. Specimens are identified by accession number when available, and when the specimen has no accession number, then if possible by bar code number, which is given here inside brackets to distinguish it from the accession number. Additional collection data for the specimens cited here and information about additional specimens not cited here are also available in the online database TROPICOS (<http://www.tropicos.org>), along with high-resolution digital images of some type specimens and selected reference specimens of most of the species treated here; the images can be accessed either by taxonomic name or by collector and number of the specimen that is imaged.

CONSERVATION STATUS ASSESSMENT METHODOLOGY

The study presented here is taxonomic and floristic: the objective is enumeration of the species that belong to this genus in the area of tropical Central and South America. This study is based on nonexhaustive survey of specimens collected over a number of years using varied survey methods aimed at various objectives, and the floristic information given here is a simplified presence report based on

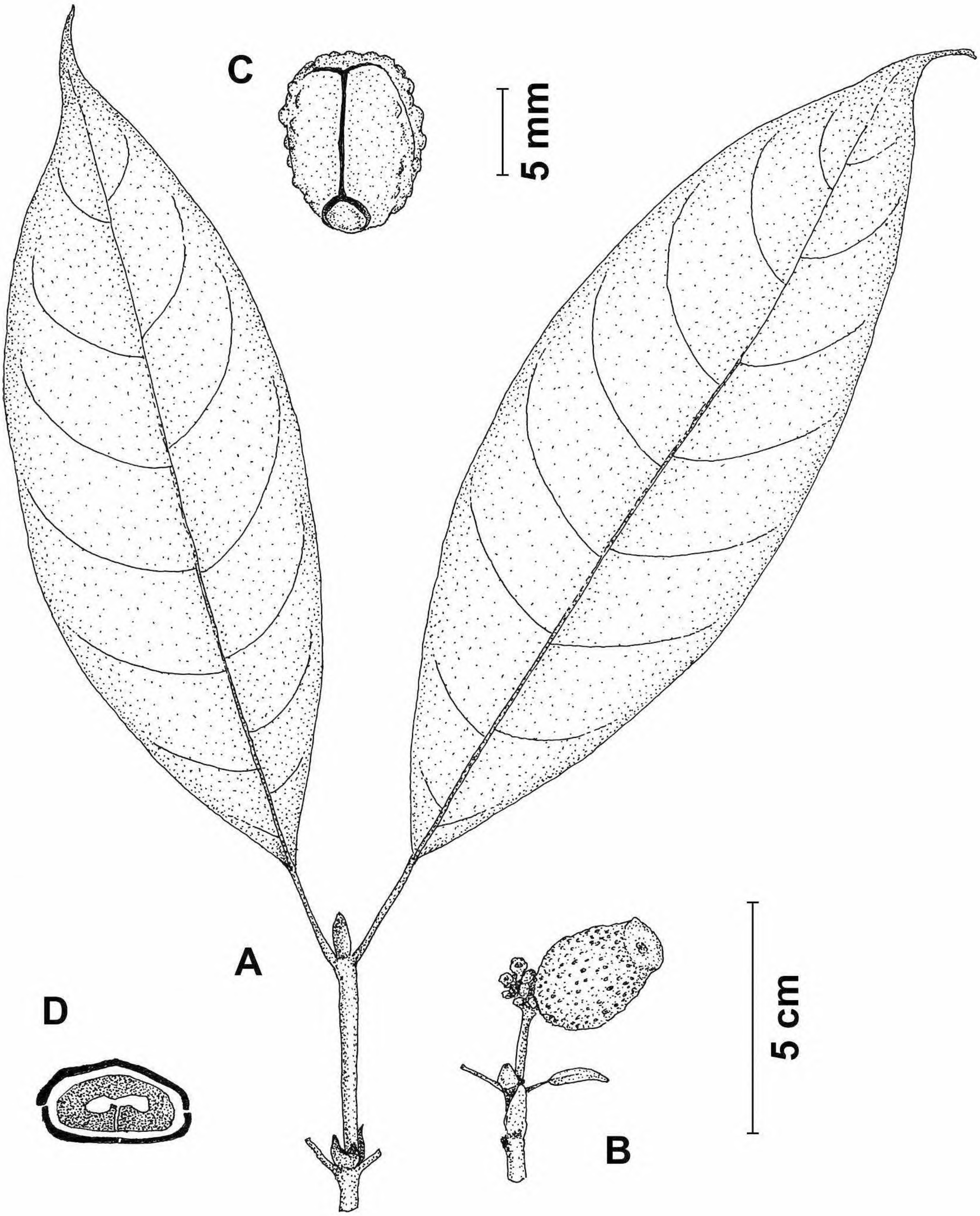


Figure 2. *Carapichea verrucosa* C. M. Taylor (*Stachyococcus* group). —A. Apical portion of vegetative stem. —B. Apical portion of stem with infructescence, with fully developed leaves removed. —C. Pyrene, based on *Mathias & Taylor 5015* (MO). —D. Schematic cross-section of pyrene, based on *Medeiros et al. 476* (MO). A, B to same 5-cm scale and based on the type *Rimachi 12346* (MO).

the available data, which are uneven and incomplete for this region (Schulman et al., 2007), and no field studies have been done targeting the occurrence of this species where it is known or expected to grow. Knowledge of the true geographic range and the population size and dynamics of a species are essential to understanding the threats to its existence and thus its actual conservation status; documenta-

tion of the existence of a species based only on museum collections does not provide data to evaluate these factors completely. A conservation assessment is provided here for this newly described species using IUCN Red List categories and criteria (IUCN, 2001) based on the totality of our current knowledge, and the basis for this assessment in the form of a map and the calculated assessment parameters is available under the corresponding species names in TROPICOS (assessment parameters are reported in the text accompanying the image). The assessment parameters were calculated using the IUCN rating tool (Moat, 2007) in ArcView GIS 3.2 (ESRI, 1999) with the grid cell size used for calculating area of occupancy (AOO) varied between 1.00 and 3.16 km depending on characteristics of the species and data (IUCN, 2011). This assessment is not being submitted to IUCN for publication in the Red List.

TAXONOMIC TREATMENT

The species of *Carapichea* are here organized into informal species groups that are morphologically separated and characterized, but these groups are not formally named. The informal groups are designated with Roman numerals, and the first two are treated in the order in which they are placed on Andersson's (2002a) phylogeny with the following groups sequenced based on morphological similarity to the previous group. Within each informal group, the species are arranged in alphabetical order. The species are numbered sequentially throughout the treatment. The species are listed alphabetically in Appendix I.

Carapichea Aubl., Hist. Pl. Guian. 1: 167, t. 64. 1775, nom. rej. versus *Cephaelis* Sw., 1788, nom. cons. *Chesnea* Scop., Intr. Hist. Nat. 119. 1777, nom. superfl. illeg. *Nettlera* Raf., Sylva Tellur. 147. 1838, nom. superfl. illeg. TYPE: *Carapichea guianensis* Aubl.

Ipecacuanha Arruda, in Koster, Trav. Brazil 497. 1816, nom. nud. Species: *Ipecacuahna officinalis* Arruda, nom. nud.

Ipecacuanha Raf., Sylva Tellur. 147. 1838. TYPE: *Ipecacuanha fusca* Raf.

Uragoga L. ex Baill., Adansonia 12: 323. 1879, nom. superfl. illeg. for *Cephaelis* Sw. TYPE: *Uragoga ipecacuanha* (Brot.) Baill. (lectotype, designated by Petit [1964: 16]).

Stachyococcus Standl., Publ. Field Mus. Nat. Hist. Bot. Ser. 13(6): 144. 1936, syn. nov. TYPE: *Stachyococcus adinanthus* (Standl.) Standl.

Psychotria ser. *Altsonii* Steyerm., Mem. New York Bot. Gard. 23: 555. 1972, syn. nov. TYPE: *Psychotria altsonii* (Sandwith) Steyerm.

Shrubs and small trees, with raphides, usually glabrous, drying greenish gray, grayish brown, yellowish brown, brown, or greenish brown; internodes weakly flattened to rounded. Leaves opposite or sometimes whorled (*Carapichea tillettii*), distichous, without domatia or with a line of pubescence along abaxial sides of midrib, venation pinnate, sometimes secondary and higher-order venation not visible (*Altsonii* group), sometimes with numerous well-developed intersecondary veins (*Pacimonica* group), sometimes apparently without intersecondary veins (some species of *Carapichea* group); stipules interpetiolar, generally persistent on distalmost nodes, with age (i.e., at lower nodes) becoming dried, starting from margins, and sometimes indurated in upper parts or throughout, then falling through fragmentation, often leaving well-developed scar or persistent hardened basal portion, apparently eglandular, adaxially glabrous, generally triangular to broadly ovate or rounded-truncate, entire, minutely bifid, shallowly to deeply 2-lobed, or sometimes deeply laciniate (*Ipecacuanha* group). Inflorescences terminal, sometimes becoming displaced to pseudoaxillary (i.e., lateral) after anthesis, sessile to pedunculate, green, white, red, pink, or purple, compactly branched and headlike (i.e., capitate) to almost headlike (i.e., subcapitate), spiciform, or thyrsiform and branched to 1 or 2 orders, with axes 2 to 4 per node, bracteate; bracts reduced (*Stachyococcus* group) to well developed, sometimes with basalmost (i.e., outermost) bracts involucral, enlarged, free or shortly to completely fused bracteoles subtending flowers reduced or sometimes replaced by glandular projections (*Altsonii* group) or pubescence (*Pacimonica* group, *Carapichea* group). Flowers bisexual, at least sometimes distylous, sessile to very shortly pedicellate; calyx limb developed, 5-lobed or sometimes truncate (*Panurensis* group, *C. pacimonica*); corolla tubular to funnelform, white, yellow, orange, salmon-pink, or purple, internally glabrous or variously pubescent, tube straight, lobes 5, valvate in bud, smooth or abaxially thickened or with hornlike appendage (*C. araguariensis*); stamens 5, inserted in corolla tube, included or exserted, anthers ellipsoid-oblong, dehiscent by longitudinal slits, pollen aperturate; ovary inferior, 2-locular, ovules 1 per locule, basal; stigmas 2, linear, included or exserted. Fruit drupaceous, subglobose to ellipsoid, fleshy, yellow, brownish yellow, orange, red, dark red, dark purple, maroon, dark blue, white, or cream, sometimes with pedicel or stipe elongating during maturation; pyrenes 2, hemispherical (i.e., planoconvex), 1-locular, bony, flat or sometimes

longitudinally twisted (*C. ipecacuanha*), dehiscent by 3 or 4 PGSs along abaxial ridges, or by a partial adaxial slit (*C. ipecacuanha*), or by a single basal-adaxial slit (*C. lucida*), or by a basal or raphal plug and sometimes also short marginal slits (*C. adinantha*, *C. verrucosa*), abaxially smooth or with 1 central crest or 3 to 5 angles or ridges, adaxially plane or with a narrow to broad, open to covered central furrow (i.e., groove) along part to all of length.

Carapichea includes at least 23 Neotropical species in understory of wet tropical forests at elevations of 50–1570 m, and has been collected from eastern Nicaragua to Bolivia, and in Venezuela, the Guianas, and eastern Brazil.

Key to Species of *Carapichea*

1a. Stipules laciniate, with 3 to 8 projections or lobes linear, 5–10 mm long; pyrenes longitudinally twisted, smooth or with a single ridge abaxially; herbs and subshrubs to 0.5 m tall with extensive rhizomes; widespread ..... *C. ipecacuanha* (species group I)

1b. Stipules entire or 2-lobed, the lobes when present triangular to linear, 5–6 mm long; pyrenes straight, smooth to angled or ridged abaxially; herbs, subshrubs, woody shrubs, or small trees, to 4 m tall, apparently not markedly rhizomatous; Costa Rica to Bolivia and eastern Brazil.

2a. Inflorescences capitate.

3a. Stipules deeply bilobed; eastern Brazil (Bahia) ..... *C. lucida* (VII)

3b. Stipules entire and truncate, rounded, obtuse, or acute to shortly bilobed; Costa Rica to Bolivia and northeastern South America.

4a. Inflorescences with bracts reduced, to 1 mm long; fruits spongy with warty surface, white to cream or brownish yellow, 15–30 mm long; pyrenes 10–20 mm long, abaxially verrucose .... *C. verrucosa* (VI)

4b. Inflorescences with developed bracts 2–70 mm long; fruits juicy with smooth surface, dark red, maroon, dark purple, dark blue, or white, 5–15 mm long; pyrenes 3–12 mm long, abaxially smooth or with longitudinal ridges.

5a. Inflorescences with external bracts 50–70 mm long, fused for more than half their length into a funnelform tube ..... *C. urniformis* (VI)

5b. Inflorescences with external bracts 8–30 mm long, free or fused for less than half their length into a cupular tube.

6a. Inflorescences enclosed by two external bracts ca. twice or more as long as remaining bracts, these external bracts ovate, lanceolate, spatulate, or pandurate, at apex acute.

7a. Inflorescences with the 2 external bracts lanceolate, spatulate, or pandurate, with peduncle 0.8–3.5 cm long; leaves of flowering branches 3.5–7 cm wide ... *C. guianensis* (II)

7b. Inflorescences with the 2 external bracts ovate, with peduncle 2–12 cm long; leaves of flowering branches 4–12.5 cm wide.

8a. Leaves of flowering branches 6–12.5 cm wide; stipules 8–15 mm long ..... *C. dolichophylla* (II)

8b. Leaves of flowering branches 4–4.3 cm wide; stipules 21–22 mm long. ..... *C. fimbriflora* (III)

6b. Inflorescences enclosed by several external bracts less than twice as long as remaining bracts, these external bracts linear, narrowly triangular, narrowly spatulate, elliptic, oblanceolate, lanceolate or ovate, at apex acute, obtuse, rounded, or truncate.

9a. Inflorescences with external bracts linear to narrowly triangular or narrowly spatulate, 1–4 mm wide; leaves with intersecondary veins well developed, with 1 to 4 intersecondary veins present between each pair of secondary veins, with 1 or more intersecondary veins more than half as long as secondary veins.

10a. Inflorescences with largest bracts narrowly triangular and 8–12 mm long ... *C. crebinervia* p.p. (III)

10b. Inflorescences with largest bracts narrowly spatulate to linear and 10–30 mm long.

11a. Outermost inflorescence bracts at base straight-sided and not sheathing; plants often drying with gray cast ..... *C. ligularis* (III)

11b. Outermost inflorescence bracts at base widened and shortly sheathing; plants often drying yellowish brown ..... *C. pacimonica* (III)

9b. Inflorescences with external bracts spatulate, elliptic, oblanceolate, lanceolate, or ovate, 5–20 mm wide; leaves with intersecondary veins not visible or few and all less than half as long as secondary veins.

12a. Leaves with secondary veins visible on adaxial surface; inflorescence with 6 to 20 external bracts ..... *C. affinis* (II)

12b. Leaves with secondary veins not visible on adaxial surface; inflorescence with 4 or 5 external bracts.

13a. Inflorescence with peduncle 9.5–17 cm long and bracts green or white often tinged with pink or purple; calyx limb subtruncate to shortly irregularly lobed ..... *C. altsonii* (IV)

13b. Inflorescence bracts with peduncle 2.5–4 cm long and bracts white; calyx limb shortly to deeply, irregularly or regularly lobed.

14a. Calyx lobes lanceolate to ovate-triangular, 0.7–1.2 mm long, acute to acuminate; corolla tube 16–19 mm long ..... *C. nivea* (IV)
14b. Calyx lobes irregular, triangular, 0.2–0.8 mm long, obtuse to rounded; corolla tube 9–11 mm long ..... *C. sandwithiana* (IV)

2b. Inflorescences with primary axis at least shortly developed and sometimes also secondary and tertiary axes developed.
15a. Inflorescences spiciform, with primary axis well developed and flowers borne in glomerules directly from it, or some flowers borne on secondary axes 1–5 mm long and much shorter than primary axis.
16a. Inflorescences shortly developed, with flowers borne at apex and 1 lower node; stipules 5–18 mm long; fruit 5–8 mm long ..... *C. panurensis* p.p. (V)
16b. Inflorescences more developed, with flowers borne at apex and at 4 to 15 lower nodes; stipules 2–5 mm long; fruit 10–15 mm long ..... *C. adinantha* (VI)
15b. Inflorescences cymose, with secondary axes and sometimes tertiary axes developed and flowers mainly borne on these, longest secondary axes 6–30 mm long and shorter than to as long as primary axis.
17a. Leaves with intersecondary veins well developed, with 1 to 4 intersecondary veins present between each pair of secondary veins, with 1 or more of these intersecondary veins more than half as long as secondary veins.
18a. Inflorescence with outermost bracts subequal or a little unequal, with the outermost bracts that subtend a group of flowers less than twice as long as next longest bracts ..... *C. crebinervia* p.p. (III)
18b. Inflorescence bracts markedly unequal, with the outermost bracts that subtend a group of flowers more than twice as long as next-longest bracts.
19a. Outermost bracts subtending flower groups 10–15 mm long ..... *C. araguariensis* (III)
19b. Outermost bracts subtending flower groups 20–25 mm long ..... *C. necopinata* (III)
17b. Leaves with intersecondary veins not visible or few and weak and all less than half as long as secondary veins.
20a. Inflorescences with bracts reduced, not covering ovaries of flowers nor enclosing groups of flowers; leaves with secondary veins not visible on abaxial surface ..... *C. panurensis* p.p. (V)
20b. Inflorescences with at least some bracts developed, covering ovaries of some or all flowers individually and/or enclosing groups of flowers; leaves with secondary veins weakly evident to clearly evident on abaxial surface.
21a. Calyx limb 2–3.5 mm long.
22a. Corolla with tube 15–16 mm long and lobes ca. 10 mm long; inflorescence with bracts equal to unequal in size ..... *C. maturacensis* (II)
22b. Corolla with tube 5–7 mm long and lobes 4–4.5 mm long; inflorescence with bracts generally similar in size ..... *C. vasivensis* (II)
21b. Calyx limb 0.8–1 mm long.
23a. Leaves drying leathery; stipules generally smooth; inflorescence with bracts 3–4 mm long; corolla with tube ca. 6 mm long and lobes ca. 3.5 mm long ... *C. tillettii* (V)
23b. Leaves drying papery; stipules generally costate; inflorescence with bracts 5–7 mm long; corolla with tube ca. 4 mm long and lobes 1.2–1.5 mm long (corolla unknown in *C. franquevilleana*).
24a. Stipules emarginate to shallowly 2-lobed when young; plants of southern Venezuela and southeastern Colombia ..... *C. franquevilleana* (II)
24b. Stipules acute to obtuse when young, though sometimes tardily splitting when old; plants of northeastern Peru ..... *C. klugii* (II)

I. *Ipecacuanha* Group

This group comprises one species found widely in lowland wet forests of Central and South America (Oliveira et al., 2010), though its native range may have been expanded by cultivation. This species is unusual in *Carapichea* in its low rhizomatous habit, deeply laciniate stipules, and longitudinally twisted pyrenes. The leaves lack acarodomatia, and the intersecondary veins, tertiary veins, and higher-order venation are not visible. This species is distylous as documented by Camargo de Assis and Giulietti (1999) and Rossi et al. (2005). The fruits are usually described by collectors as dark red but rarely as blue.

Its systematic position was controversial for many years, but its relationship to species included in *Carapichea* has been demonstrated by molecular sequence data (Andersson, 2002a; Bremer & Eriksson, 2009). This species was not treated by Steyermark (1972) in his study of Psychotrieae in northeastern South America.

1. Carapichea ipecacuanha (Brot.) L. Andersson, Kew Bull. 57: 371. 2002. Basionym: *Callicocca ipecacuanha* Brot., Trans. Linn. Soc. 6: 137. 1802. *Psychotria ipecacuanha* (Brot.) Stokes, Bot. Mat. Ned. 1: 365. 1812. *Cephaelis ipecacuanha* (Brot.) A. Rich., Bull. Fac. Med. 4: 92. 1818. *Uragoga ipecacuanha* (Brot.) Baill., Hist. Plant. 7: 370. 1880. *Evea ipecacuanha* (Brot.) W. Wight, Contr. U.S. Natl. Herb. 9: 216. 1905; *Evea ipecacuanha* (Brot.) Standl., Contr. U.S. Natl. Herb. 18: 123. 1916, isonym, nom.

inval. TYPE: Tab. 11 in Brot., Trans. Linn. Soc. 6: t. 11, 1802 (lectotype, designated by Boer & Thulin [2005 (2006): 1081]).

Ipecacuanha fusca Raf., Sylva Tellur. 147. 1838. TYPE: not designated.

Cephaelis acuminata H. Karst., Deut. Fl. 1196. 1883. *Uragoga acuminata* (H. Karst.) Farw., Druggist's Circ. 61: 175. 1917, nom. illeg., non *Uragoga acuminata* (Benth.) Kuntze, Revis. Gen. Pl. 1: 299. 1891. TYPE: Colombia. Chocó: mun. Riosucio, zona de Urabá, cerros del Cuchillo, camino de Cidon a la cumbre sureste, 50–100 m, 23 June 1988, *D. Cárdenas 2093* (neotype, designated by Boer & Thulin [2006: 1081], JAUM not seen; isoneotypes, HUA not seen, MO-4049656!).

This species is found from Nicaragua sporadically to eastern Brazil in wet forests at elevations of 0–400 m. Oliveira et al. (2010) found that the geographic distribution of this species is fragmented with markedly different levels of genetic and chemical diversity in different populations. A morphological description and illustration of this species were provided by Burger and Taylor (1993: 255, fig. 13, as *Psychotria ipecacuanha*), and a description by Taylor (2001b: 2265–2266, as *P. ipecacuanha*). The morphological variation of this species in Brazil was extensively documented and illustrated by Camargo de Assis and Giulietti (1999, as *P. ipecacuanha*), and its phenology was studied by Rodrigues et al. (1995).

This species has long been the principal source of the vomitory drug ipecac, which is derived from its well-developed rhizomes. Boer and Thulin (2005) listed various pharmaceutical names that have been used for this species.

II. *Carapichea* Group

This group includes seven species found in lowland wet to seasonal forests at elevations of 20–1570 m, from southern Central America to Bolivia and through the Guianas and the Amazon basin to southeastern Brazil. These species share well-developed, entire to bilobed stipules, a usually grayish or brownish gray drying color, capitate to branched inflorescences with well-developed peduncles and well-developed bracts, and usually purple to blue-black fruits. The leaves have well-developed secondary veins but lack visible intersecondary veins and often the tertiary and higher-order venation are not visible. Acarodomatia appear to be lacking. The stipules are generally ovate to triangular-ligulate, and variously entire, minutely bifid, or bilobed, sometimes with this variation all found in the same species (e.g., *C. guianensis*). The inflorescence bracts are generally equal in size or have a regular gradation from largest to smallest except in *C. guianensis* and *C. dolichophylla*, which have a pair of markedly larger outermost bracts that are twice or more as large as the next largest bracts. The inflorescence bracts are generally described as green, white, pink, red, purple, or lilac during flowering and as green, red, or purple during fruiting. The flowers are generally subtended by dense sericeous or lanose pubescence and are apparently distylous. The corollas are white and often have abaxial thickenings or horns on the lobes. The fruits are described as red-orange maturing to black (*C. guianensis*, *Clarke 4366*, MO!) or maturing to orange, dark red, dark purple, violet, or purple-black.

This species group includes the type of *Carapichea*, *C. guianensis*, which has been treated taxonomically in different ways. Steyermark (1972, 1974) included these plants as one of two varieties of *Psychotria ligularis*, as *P. ligularis* var. *carapichea*. However, Delprete (2001) noted that Steyermark's varieties are better regarded as two different species and the other, *C. ligularis* (= *P. ligularis* var. *ligularis* of Steyermark) is here included as a species belonging to a different group, the *Pacimonica* group. Steyermark classified *C. guianensis* (1972; as *P. ligularis* var. *carapichea*) in his *Psychotria* sect. *Cephaelis* (Sw.) Müll. Arg. and its *Psychotria* ser. *Cephaelis* Steyerm. (Steyermark [1972: 668] here appears to have incorrectly regarded his *Psychotria* ser. *Cephaelis* as an autonymic name because it included the type species of the name of its higher taxon, *Psychotria* sect. *Cephaelis*; however, this section does not include the type of the genus, and thus is not an autonym. Even though he treated this series as an autonym, Steyermark did provide a Latin diagnosis and designated a type, so he is the author of this name.) Three of the species included in the *Carapichea* group, *C. franquevilleana* (Müll. Arg.) C. M. Taylor, *C. vasivensis*, and *C. maturacensis*, were classified by Steyermark (1972) in his unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574) and its unnamed and undiagnosed *Psychotria* ser. A (1972: 574) together with another species that is not transferred to *Carapichea*, *P. wurdackii* Steyerm.

2. Carapichea affinis (Standl.) L. Andersson, Kew Bull. 57(2): 371. 2002. Basionym: *Cephaelis affinis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(3): 184. 1930. TYPE: Peru. Loreto: betw. Yurimaguas & Balsapuerto, 26–31 Aug. 1929, *E. P. Killip & A. C. Smith 29329* (holotype, US-1356290, US digital image!; isotype, F-612034, F digital image!).

Cephaelis borucana Ant. Molina, Ceiba 4: 31. 1951. *Psychotria borucana* (Ant. Molina) C. M. Taylor & W. C. Burger, Monogr. Syst. Bot. Missouri Bot. Gard.

45: 1258. 1993. TYPE: Costa Rica. Puntarenas: cantón de Osa, near Esquinas Experimental Station, area betw. Río Esquinas & Palmar Sur de Osa, 200 ft., 11 May 1950, *P. H. Allen 5340* (holotype, US-2215926 digital image!; isotypes, F-174638 digital image!, US-2086253 digital image!).

This species is known from wet lowland, premontane, and lower montane forests at elevations of 20–1570 m, in southern Costa Rica and from the western Amazon basin of Colombia to Bolivia and into western Brazil. A modern description and illustration of this species were presented by Burger and Taylor (1993: 236, fig. 17; as *Psychotria borucana*) and a description by Taylor (1997b: 626, as *P. borucana*). The inflorescences of this species are densely capitate but often become somewhat lax as the fruits mature, with the receptacle broadening and sometimes the inflorescence axes shortly developing. This species is similar to *Carapichea dolichophylla*; see additional comments about their separation in the discussion of that species.

3. Carapichea dolichophylla (Standl.) C. M. Taylor, Fl. Ecuador 79: 6. 2006. Basionym: *Cephaelis dolichophylla* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 334. 1929. *Psychotria dolichophylla* (Standl.) C. M. Taylor, Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1258. 1993. TYPE: Peru. Loreto: prope Yurimaguas ad flumen Huallaga, Peruviae orientali, May 1855, *R. Spruce 3876* (holotype, K[000006657], K digital image!; isotype, K[000006656], K digital image!).

This species is known from wet forests at elevations of 100–900 m in the western Amazon basin, from Colombia to Bolivia and western Brazil. A modern description was presented by Taylor (1997b: 627; as *Psychotria dolichophylla*). This species is similar to *Carapichea affinis*, which has a broader geographic range and is more commonly collected. These two species are distinguished by features of the inflorescence: in *C. dolichophylla* the bracts are acute to obtuse and clearly angled at the apex, and the inflorescences are fully enclosed by a pair of external bracts that are markedly larger than the other bracts and described as green, pink, or usually red in flower and green to occasionally purple or usually red in fruit; while in *C. affinis* the bracts are broadly obtuse to rounded at the apex, and the inflorescence is surrounded by two or three pairs of bracts, with no pair of bracts completely enclosing the head nor markedly larger than the others, and the inflorescence bracts are described as green or infrequently pink in flower and becoming purple in fruit.

Two specimens of Spruce's collection #3876 deposited at K are available for study as digital images. The specimen annotated in Standley's handwriting as "*Cephaelis dolichophylla* Standl. Type" is here considered the holotype, and the duplicate specimen that has no annotation by Standley is considered an isotype.

4. Carapichea franquevilleana (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Psychotria franquevilleana* Müll. Arg., Fl. Bras. 6(5): 325. 1881. *Uragoga franquevilleana* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 960. 1891. TYPE: Venezuela. Amazonas: in regione Rio Negro ad flumen Pacimoni in montanis, Feb. 1854, *R. Spruce 3378* (holotype, P in Herbarium Franqueville not seen, P in Herbarium Franqueville as photo F neg. #37238 at MO!; isotypes, G!, G as photo F neg. #25785 at MO!, K[00043841], K digital image!).

This species is known from lowland vegetation at elevations of ca. 250 m in southern Venezuela and southeastern Colombia. The collection locality was ascribed to Brazil by Spruce, but Steyermark (1972: 580) clarified that it is today in Venezuela. In addition to the locality information given in the protologue, cited above, the label adds the specific locality "in sylvis pedem montis Imei."

This species is poorly known and is treated provisionally here following Steyermark (1972, 1974). It was originally described as based on a specimen without flowers or fruits, with details of the flowers added by Steyermark based apparently on a single specimen from Colombia (*H. García-Barriga 13939*, no herbarium cited, not seen). A morphological description was presented by Steyermark (1974: 1444–1446), and later re-stated by Taylor et al. (2004: 739). Steyermark's description expanded the morphological variation included in this species, in particular in the calyx limb that he noted ranges to repand-truncate with rounded projections, while the protologue described the calyx limb as truncate, the condition found on the type collection. Steyermark also described the form of the corollas, but their size is still unknown.

In general aspect *Carapichea franquevilleana* is similar to *C. vasivensis*, which is known from the same region in Venezuela. Steyermark (1972: 580) distinguished *C. franquevilleana* by its glabrous inflorescences with secondary axes verticillate in contrast to pubescent inflorescences with paired axes in *C. vasivensis*. Steyermark confused *C. vasivensis in herb.* with *C. maturacensis*, but both of these differ in their pubescent inflorescences from *C. franquevilleana*.

Carapichea franquevilleana is also similar, including in the glabrous inflorescences of similar form, to *C. klugii* of the western Amazon basin; these species are separated here provisionally as discussed under *C. klugii*.

5. Carapichea guianensis Aubl., Hist. Pl. Guiane 1: 168, tab. 64. 1775. *Callicocca guianensis* (Aubl.) J. F. Gmel., Syst. Nat. 2(1): 372. 1791; as "gujanensis." *Tapogomea carapichea* Poir., Encycl. 7: 587, tab. 152, fig. 3. 1806, nom. superfl. illeg. *Cephaelis involucrata* Willd., Sp. pl. 1: 979. 1798, nom. superfl. illeg. *Carapichea aubletii* DC., Prodr. 4: 536. 1830, nom. superfl. illeg. *Nettlera guianensis* (Aubl.) Raf., Sylva Tellur. 147. 1838. *Uragoga involucrata* (Willd.) Kuntze, Revis. Gen. Pl. 2: 956. 1891, nom. superfl. illeg. *Uragoga guianensis* (Aubl.) Pulle, Enum. Vasc. Pl. Surinam 446. 1906. *Cephaelis guianensis* (Aubl.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 335. 1929. *Psychotria ligularis* var. *carapichea* Steyerm., Mem. New York Bot. Gard. 23: 676. 1972. *Psychotria carapichea* (Steyerm.) Delprete, Brittonia 53: 401, fig. 2. 2001, non *Psychotria guianensis* (Aubl.) Raesch., 1796. TYPE: French Guiana. Dans les grandes forêts qui aboutissent à la crique des Galibis, en fleur et en fruit Mai, *Aublet s.n.* (holotype, BM not seen).

Psychotria galbaoensis Steyerm., Brittonia 33: 387. 1981. TYPE: French Guiana. Pente nord-est des monts Galbao, a 10 km au SO de Saül, 500–600 m, 11 Mar. 1975, *J. J. de Granville 2383* (holotype, VEN not seen; isotypes, CAY not seen, MO-2798770!, MO-3332374!).

This species is known from wet forests at elevations of 150–710 m in Guyana, Surinam, French Guiana, and northern Brazil. Its systematic relationships were not clear until *Carapichea* was recognized in its modern circumscription (Andersson, 2002a). The flowers described and seen resemble the short-styled form of distylous flowers. The pyrenes sometimes have two adaxial longitudinal chambers, an unusual form. A recent description and illustration were presented by Boom and Delprete (2002; as *Psychotria carapichea*), and that same illustration was also published by Delprete (2001: 402, fig. 2; also as *P. carapichea*).

Steyermark (1972) classified these plants as a variety of *Psychotria ligularis*, which he called *P. ligularis* var. *carapichea*. He subsequently described *P. galbaoensis* based on plants from the type region of *Carapichea guianensis*, without contrasting his new species to *P. ligularis* var. *carapichea*. Delprete (2001, 2003) noted that Steyermark's varieties of *P. ligularis* are better treated as two separate species and that *P. galbaoensis* was a synonym of *C. guianensis* and published the name *P. carapichea* (Steyerm.) Delprete for *P. ligularis* var. *carapichea*. Delprete's name was originally published (2001) as "*P. carapichea* (Poir.) Delprete," with *Tapogomea carapichea* Poir. as the basionym. However, Poiret's name is illegitimate and thus not available as a basionym. Therefore, *P. carapichea* could have been considered a replacement name authored solely by Delprete, but Delprete subsequently (2003) corrected the authorship of this name to cite *P. ligularis* var. *carapichea* Steyerm. as the basionym and Steyermark as the parenthetical author. The typification cited here for *C. guianensis* follows Delprete (2003).

6. Carapichea klugii (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria klugii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(5): 377. 1931. TYPE: Peru. Loreto: in forest, Mishuyacu near Iquitos, alt. 100 m, Jan. 1930, *G. Klug 835* (holotype, F-612590; isotype, NY[00132715], NY digital image!).

This species is known from both terra firme and seasonally inundated wet vegetation on various substrates, including very often white sands, at elevations of 122–200 m in the western Amazon basin of Peru and perhaps southern Colombia. This species shows some variation in the drying color of its specimens, which generally are either yellowish brown or dark brownish gray. However, these two drying-color forms are morphologically indistinguishable, and both have been collected at several sites (e.g., Peru, Mishana, Río Nanay: *F. Ayala 5995*, *M. Rimachi Y. 2239*, yellowish brown; *F. Ayala et al. 3207*, *M. Rimachi Y. 4167*, brownish gray); further study will be necessary to understand this variation. The inflorescences vary in size and form in this species, apparently with age: they are generally rather small and densely bracteate in flower, then the axes become more elongated and robust and the bracts fall off as the fruits develop.

Carapichea klugii is similar to *C. franquevilleana*. These two species differ in their stipule shape, emarginate to bilobed in *C. franquevilleana* in contrast to acute to obtuse in *C. klugii*, and they are apparently geographically separated, with *C. franquevilleana* found in the northern and northeastern Amazon basin and *C. klugii* in the western Amazon basin. Stipule shape is highly variable within some other species of *Carapichea* (e.g., *C. guianensis*) and may not be a good indication of species distinctions but may be consistent within some species. No other morphological differences are

evident between these; *C. franquevilleana* is very poorly known, and the area between their known ranges is poorly explored botanically. Therefore, these species are provisionally separated here.

7. Carapichea maturacensis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria maturacensis* Steyerm., Mem. New York Bot. Gard. 23: 578, fig. 78. 1972. TYPE: BRAZIL. Amazonas: betw. Missão Salesiana & Serra Pirapucú, on Rio Maturacá, 50–400 m, 15 Jan. 1966, *N. T. Silva & U. Brazão 60842* (holotype, NY[00132736], NY digital image!).

This species is found in scrubby or seasonal lowland vegetation at elevations of 50–400 m on nutrient-poor, often sandy soils in southern Venezuela and adjacent northern Brazil. A description and illustration were presented by Steyermark (1974: 1442–1444, fig. 236; as *Psychotria maturacensis*) and a description by Taylor et al. (2004: 746–747; as *P. maturacensis*). This species has sometimes been confused with *Carapichea vasivensis*, which is similar in general morphology but differs markedly in its corolla size, as outlined in the Key to Species, and also apparently in habitat.

8. Carapichea vasivensis (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Mapouria vasivensis* Müll. Arg., Flora 59: 460, 466. 1876. *Uragoga vasivensis* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 963. 1891. *Psychotria vasivensis* (Müll. Arg.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7(4): 461. 1931. TYPE: Venezuela. Amazonas: ad flumen Casiquiare, Vasiva et Pacimoni, 1853–1854, *R. Spruce 3334* (holotype, M not seen; isotypes, C not seen, C as photo F neg. #22854 at MO!, G!, NY[00132243], NY digital image!).

This species is known from wet vegetation of seasonally inundated riversides at elevations of 100–150 m in southern Venezuela. The collection locality was ascribed to Brazil by Spruce, but Steyermark (1972) clarified that it is today in Venezuela. A description and illustration were presented by Steyermark (1974: 1436–1439, fig. 234; as *Psychotria vasivensis*) and by Taylor et al. (2004: 762, fig. 587; also as *P. vasivensis*). This species has sometimes been confused with *Carapichea maturacensis*, which is similar in its general morphology but differs markedly in its corolla size, with the tube 15–16 mm long and the lobes ca. 10 mm long in *C. maturacensis* in contrast to the tube 5–7 mm long and the lobes 4–4.5 mm long in *C. vasivensis*; also *C. maturacensis* is apparently found in wet vegetation in seasonally inundated habitats.

III. *Pacimonica* Group

This group comprises six species found in wet lowland to premontane vegetation at 50–800 m in northeastern South America. These species share a distinctive yellowish gray or gray-brown drying color, leaves with numerous well-developed intersecondary veins and the tertiary and quaternary venation hardly or not visible, relatively short truncate to broadly 2-lobed stipules, well-developed peduncles, and subcapitate to shortly branched inflorescences with green bracts of markedly different lengths with the longest bracts narrowly ligulate to linear, except in *Carapichea fimbriflora* (Steyerm.) C. M. Taylor where they are broader. The leaves lack tufted acarodomatia in the abaxial axils of the secondary veins, but abaxially there is usually a line of short pilosulose pubescence along each side of the midrib, which may serve a similar function. *Carapichea pacimonica* and *C. araguariensis* have distylous flowers; the floral biology of the other species is unknown. The corollas are described as white, salmon-pink, orange, or purple, and their lobes usually have well-developed abaxial thickenings or horns. The mature fruits are reported to be red, yellow, or most often orange and are often borne on stipes, which develop as the fruits mature.

Two of the species included here, *Carapichea araguariensis* and *C. pacimonica*, were classified by Steyermark (1972; as *Psychotria araguariensis* Steyerm. and *P. pacimonica* Müll. Arg., respectively) in *Psychotria* subg. *Heteropsychotria* and in his unnamed and undiagnosed *Psychotria* sect. 7 (1972: 574), and its unnamed and undiagnosed *Psychotria* ser. C (1972: 588) along with several other species that apparently do not belong to *Carapichea*. Steyermark classified *C. ligularis* (1972; as *P. ligularis*) in *Psychotria* sect. *Cephaelis* ser. *Cephaelis* along with *C. fimbriflora* (Steyermark, 1981; as *P. fimbriflora* Steyerm.). As discussed previously for the *Carapichea* group, Steyermark circumscribed *P. ligularis* to include two varieties that are here considered to represent separate species, *C. ligularis* of this species group and *C. guianensis* of the *Carapichea* group. Steyermark's species *P. fimbriflora* is poorly known and is provisionally classified here based on Steyermark's note that this species is most closely related to *P. ligularis*; however, he did not specify to which variety of *P. ligularis*. These two varieties or species differ in the pattern of leaf venation and the pubescence of the lower leaf surface, and although Steyermark did not describe

the leaf venation of *P. fimbriflora* he did note that its leaves abaxially have a line of puberulous pubescence along each side of the midrib, which is found in *C. ligularis* but not in *C. guianensis*.

9. Carapichea araguariensis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria araguariensis* Steyerm., Mem. New York Bot. Gard. 23: 588. 1972. TYPE: Brazil. Amapa: Rio Araguari, vic. Camp 12, 1°11′N, 52°8′W, 20 Sep. 1961, *J. M. Pires, W. Rodrigues & G. C. Irvine 51371* (holotype, NY[00152398], NY digital image!).

This species is known from wet forests on terra firme at elevations of 50–125 m in northern Brazil. A description of this species was presented by Taylor et al. (2004: 595; as *Psychotria araguariensis*), and it was illustrated by Campos and Brito (1999: 627, 639; misidentified as *P. pacimonica*). *Carapichea araguariensis* is similar to *C. necopinata* (Standl.) C. M. Taylor, which is poorly known and separated provisionally here from *C. araguariensis* based on differences in the inflorescence bracts: the outermost bracts of the flower groups are 10–15 mm long in *C. araguariensis* in contrast to 20–25 mm long in *C. necopinata*.

10. Carapichea crebrinervia (Standl.) C. M. Taylor, comb. nov. Basionym: *Cephaelis crebrinervia* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 188. 1936. TYPE: Brazil. Pará: in silvis non inundatis loco Antonio Lemos prope flumen Tajapuru aestuarii amazonici, 27 Sep. 1919, *A. Ducke 15351* (holotype, B, destroyed, B as photo F neg. #49863 at F digital image!).

This species is known from seasonally flooded lowland wet forests in northern Brazil, most often near the Amazon River. It has been collected infrequently and is not well known. Additional study is needed before its typification can be clarified.

11. Carapichea fimbriflora (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria fimbriflora* Steyerm., Brittonia 33: 386. 1981. TYPE: Brazil. Amazonas: Operacão Juruá-Ponto 86-SC-18-SC, 14 Nov. 1975, *B. S. Pena* (holotype, VEN-134383, VEN digital image!).

This species is known only from the type collection, from lowland wet forests on terra firme in northern Brazil. The outermost bracts of the inflorescence were described as ovate-lanceolate and are broader than long, ca. 15 mm long and ca. 18 mm wide, in contrast to the very narrow bracts found in the other members of this species group. The flowers are reported in the protologue to be purple. On the digital image of the holotype, the inflorescence has broken off the peduncle and is not shown and may be lost.

12. Carapichea ligularis (Rudge) Delprete, Brittonia 55: 89. 2003. Basionym: *Schradera ligularis* Rudge, Pl. Guian. 1: 29, tab. 45. 1805. *Cephaelis ligularis* (Rudge) DC., Prodr. 4: 533. 1830. *Uragoga ligularis* (Rudge) Kuntze, Revis. Gen. Pl. 2: 961. 1891. *Psychotria ligularis* (Rudge) Steyerm., Mem. New York Bot. Gard. 23: 675. 1972. TYPE: Guyana. S. loc., *E. Rudge s.n.* (lectotype, designated by Delprete [2001: 399], P not seen).

This species is known from wet forests at elevations of 100–800 m in Guyana, Surinam, French Guiana, and northern Brazil. The only record for Guyana appears to be the type collection. A recent description and illustration were provided by Boom and Delprete (2002; as *Psychotria ligularis*), and that same figure was also published by Delprete (2001: 400, fig. 1; also as *P. ligularis*) who clarified its taxonomic status.

13. Carapichea necopinata (Standl.) C. M. Taylor, comb. nov. Basionym: *Psychotria necopinata* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 242. 1936. TYPE: Brazil. Amazonas: Cucuhy, Río Negro, ca. 120 m, Feb. 1930, *E. G. Holt & W. Gehriger 386* (holotype, F-625063, F digital image!; isotype, G!).

This species is known only from the type collection in lowland northern Brazil. Its elevational range and habitat (i.e., terra firme vs. flooded forest) were not recorded, and its mature flowers are unknown. This name was synonymized with *Carapichea pacimonica* by Steyermark (1972; both as *Psychotria*), but these species are separated here as outlined in the discussion of *C. pacimonica*. *Carapichea necopinata* is also similar to *C. araguariensis*, and their separation is outlined in the discussion of this last species.

14. Carapichea pacimonica (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Psychotria pacimonica* Müll. Arg., Fl. Bras. 6(5): 337. 1881. *Uragoga pacimonica* (Müll. Arg.) Kuntze, Revis. Gen. Pl. 2: 961. 1891. TYPE: Venezuela. Amazonas: in regione superiore Rio Negro ad flumen Pacimoni, Feb. 1854, *R. Spruce 3445* (holotype, M not seen; isotypes, G!, G as photo F neg. #25816 MO!, K[000432482], K digital image!).

This species is known from seasonally flooded wet forests at elevations of 100–160 m in northern Brazil and southern Venezuela. The type locality of this species was attributed to Brazil by Spruce, but its actual location in Venezuela was clarified by Steyermark (1972: 589). A description and illustration of this species were provided by Steyermark (1974: 1454–1457, fig. 240; as *Psychotria pacimonica*) and a description by Taylor et al. (2004: 750; also as *P. pacimonica*). However, the illustration presented for this species by Campos and Brito (1999: 627, 639) actually depicts *Carapichea araguariensis*. The leaves of *C. pacimonica* are notably rather thick-textured and often shiny. This species is similar to *C. ligularis*, which differs in its outermost inflorescence bracts that are not sheathing at the base in contrast to the sheathing bracts of *C. pacimonica*. *Carapichea pacimonica* is also similar to *C. crebrinervia*, which differs in its outermost inflorescence bracts that are narrowly triangular and not markedly longer than the remaining bracts in contrast to the outermost inflorescence bracts sheathing and twice or more as long as the remaining bracts in *C. pacimonica*.

Steyermark synonymized *Carapichea necopinata* with *C. pacimonica* (1972: 589; both as *Psychotria*), and Delprete (2001) agreed. Steyermark combined these species based on their similar inflorescence arrangement, pubescence, and corolla form. However, with more specimens now available, *C. necopinata* can be separated from *C. pacimonica* in its inflorescences with the secondary axes at least shortly developed and its habitat in terra firme forest in contrast to the inflorescences capitate in flower although sometimes becoming subcapitate in fruit and a habitat in seasonally flooded areas in *C. pacimonica*. Neither of these species is well documented, and Steyermark (1972) himself did not fully incorporate the morphological variation in inflorescence arrangement into his treatment: *C. pacimonica* was keyed there, as *P. pacimonica*, only as having capitate inflorescences, even though Steyermark elsewhere mentioned that this species had branched inflorescences. In practice *C. pacimonica* has been more often confused with *C. araguariensis*, as discussed under this last species.

IV. *Altsonii* Group

This group comprises four rather poorly known species found in wet lowland to lower montane escarpment forests at elevations of 80–1100 m in northeastern South America. These species share a distinctive brown drying color, relatively large leaves, broad interpetiolar stipules, capitate inflorescences with four to six well-developed involucral bracts, and shortly pedicellate flowers that lack bracts but are subtended by glandular projections of the inflorescence receptacle and/or pedicel. This inflorescence arrangement is unusual if not unique in Neotropical Psychotrieae. The leaves lack acarodomatia. Flowers have been described only for *Carapichea sandwithiana* (Steyerm.) C. M. Taylor, and although their biology is unknown, they are similar to the long-styled form of distylous species. The fruits of *C. urniformis* are reported to be bluish purple; the mature fruit color is apparently unknown for the other species.

Carapichea altsonii, *C. nivea* (Sandwith) C. M. Taylor, and *C. sandwithiana* are similar morphologically, sharing an apparently unbranched succulent habit, leaves with the venation not visible adaxially, rounded thin-textured stipules, and pedunculate inflorescences. In general aspect they resemble species of *Notopleura* subg. *Notopleura*, and Steyermark considered all the species of the *Altsonii* group related to *Notopleura*. Taylor et al. (2004) followed him and included *C. sandwithiana* in *Notopleura*, but, as detailed in the introduction, these species do not have the characters that diagnose *Notopleura*. *Carapichea urniformis* differs from the other three species of this group in its leaves with well-marked secondary and higher-order venation and its subsessile inflorescences.

15. Carapichea altsonii (Sandwith) C. M. Taylor, comb. nov. Basionym: *Cephaelis altsonii* Sandwith, Bull. Misc. Inform. Kew 1931: 475. 1931. *Psychotria altsonii* (Sandwith) Steyerm., Mem. New York Bot. Gard. 23: 555. 1972. TYPE: Guyana. Macreba Falls, Kurupung River, Mazaruni River, Aug. 1925, *R. A. Altson 322* (lectotype, designated here, K[000174497], K digital image!; isolectotype, K[000174398], K digital image!).

This species is known from wet forests at elevations of 80–400 m in Guyana. It has been collected infrequently, but was recently found again in the type locality (*B. Hoffmann et al. 2050*, MO!). This species differs from both *Carapichea nivea* and *C. sandwithiana* in its well-developed peduncles, 9.5–17 cm long, and inflorescence bracts green or white often tinged with pink or purple in contrast to the peduncles 2.5–4 cm long and the bracts white in the other two species.

16. Carapichea nivea (Sandwith) C. M. Taylor, comb. nov. Basionym: *Cephaelis nivea* Sandwith, Bull. Misc. Inform. Kew 1939: 551. 1939. *Psychotria nivea* (Sandwith) Steyerm., Mem. New York Bot. Gard. 23: 556. 1972. TYPE:

Guyana. Potaro River, Amatuk portage, on sandstone, 31 Aug. 1937, *N. Y. Sandwith 1249* (holotype, K[000174488], K digital image!; isotypes, K[000174489], K digital image!, NY-2747, NY digital image!).

This species is known from wet lowland and escarpment forests at elevations of 274–610 m in Guyana, where it has been collected infrequently. It is similar to *Carapichea altsonii*, but can be separated by its shorter peduncles, 2.5–4 cm long, inflorescence bracts flushed with white, and yellow corollas in contrast to peduncles 9.5–17 cm long and both the bracts and corollas purple in *C. altsonii*. *Carapichea nivea* is also similar to *C. sandwithiana*, but can be separated by its corollas with the tube 16–18 mm long in contrast to 9–11 mm long in *C. sandwithiana*.

Two specimens deposited at K are available for study as digital images. The specimen that has complete label data and bears the notation "Typus" in Sandwith's handwriting is here regarded as the holotype; the duplicate specimen there of this same collection that has only partial label data and no annotation as a type is considered an isotype.

17. Carapichea sandwithiana (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Cephaelis sandwithiana* Steyerm., Mem. New York Bot. Gard. 17(1): 428, fig. 42. 1967. *Psychotria sandwithiana* (Steyerm.) Steyerm., Mem. New York Bot. Gard. 23: 555. 1972. *Notopleura sandwithiana* (Steyerm.) C. M. Taylor, Fl. Venez. Guayana 8: 663. 2004. TYPE: Venezuela. Bolívar: along Río Framela, Cerro Pitón, Cordillera Epicara, Alto Río Cuyuni, Río Chicanán, 400 m, 3 Sep. 1962, *B. Maguire, J. A. Steyermark & C. K. Maguire 53562* (holotype, VEN-63029, VEN digital image!).

This species is so far known only from the type collection from wet forest at an elevation of ca. 400 m in southern Venezuela. The description presented by Taylor et al. (2004; as *Notopleura sandwithiana*) was based entirely on the protologue. This species was included in *Notopleura* by Taylor et al. (2004) based on the protologue figure that showed the inflorescence borne at the apical node alongside young leaves emerging from the stem apex, which was misinterpreted to indicate a pseudoaxillary position that supported inclusion of this species in *Notopleura*. However, further study of the species of the *Altsonii* group shows that the inflorescences are solitary and terminal and later sometimes displaced to pseudoaxillary by subsequent growth from an axillary bud but not consistently pseudoaxillary at several nodes along the stem as in *Notopleura* (Taylor, 2001a). *Carapichea sandwithiana* is similar to *C. altsonii* and *C. nivea*; its distinctions from these are summarized in the discussions of each of the other two species.

18. Carapichea urniformis (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria urniformis* Steyerm., Mem. New York Bot. Gard. 23: 556, fig. 74. 1972. TYPE: Guyana. Upper Mazaruni River basin, Mt. Ayanganna, in forest below talus along NE side, 800–900 m, 1 Aug. 1960, *S. S. Tillett, C. L. Tillett & R. Boyan 45008* (holotype, NY[00132855], NY digital image!).

This species is known from wet escarpment forests at elevations of 712–1100 m on Mt. Ayanganna in Guyana. It is notable for its capitate inflorescences enclosed by large red bracts that are fused into a vase-shaped funnelform structure. It has been collected infrequently but was found as recently as 2001 (*D. Clarke et al. 2963*, MO!).

V. *Panurensis* Group

This group comprises two species found in wet forests at elevations of 100–1570 m in the Guianas and northern Brazil. These species share stiff-textured leaves, well-developed ovate stipules, and inflorescences that are spiciform or branched to one or two orders and have relatively short bracts. Their pyrene morphology is varied: that of *Carapichea tillettii* is similar to that of some other species of *Carapichea*, while the pyrenes of *C. panurensis* are unlike any other species of *Carapichea* in their well-developed abaxial ribs. The leaves lack acarodomatia, and the secondary, intersecondary, and tertiary leaf venation is barely or not visible in both species. The stipules of *C. panurensis* are entire, whereas those of *C. tillettii* are bilobed. The bracts subtending the flower groups or secondary inflorescence axes are generally reduced; the bracts subtending the flowers are barely equal to or usually shorter than the ovary of the flowers. The flowers of both species are subtended by a ring or tuft of sericeous or pilose pubescence, which is deciduous as the fruits develop. The flowers of *C. panurensis* appear to be distylous, with the stamens partially exserted in the long-styled form and well exserted in the short-styled form; the floral biology of *C. tillettii* is unknown, but the flower described in its protologue resembles the short-styled form of distylous species. The corollas are described by collectors as white or cream and the fruits as maroon, dark purple, or dark red.

Carapichea panurensis appears not to have been treated taxonomically since it was described, when

Mueller (1881) classified it in *Mapouria* and included it in a group with several other species that are included here in *Carapichea* or have been transferred to *Margaritopsis* (Taylor, 2005). Steyermark included *C. tillettii* in *Psychotria* sect. *Chytropsia* (Bremek.) Steyerm. (1972: 484, 496; as *P. tillettii*), which comprised a heterogeneous group of species; several of those are now included in *Margaritopsis* (Taylor, 2005) and others appear to belong to *Rudgea* (Taylor et al., in prep.). The two species of the *Panurensis* group both have the characteristic stipule morphology of *Carapichea*.

19. Carapichea panurensis (Müll. Arg.) C. M. Taylor, comb. nov. Basionym: *Mapouria panurensis* Müll. Arg., Flora 59: 460. 1876. *Uragoga magnusiana* Kuntze, Revis. Gen. Pl. 2: 956. 1891, non *Uragoga panurensis* (Müll. Arg.) Kuntze, 1891. TYPE: Brazil. Amazonas: prope Panuré ad Rio Uaupes, Oct. 1852–Jan. 1853, *R. Spruce 2689* (holotype, BR!; isotypes, C not seen, C as photo F neg. #22841 at MO!, G!, P!).

This species is known from scrub forest, seasonal forest, or caatinga at elevations of ca. 100–150 m in northern Amazonian Brazil and adjacent southeastern Colombia. The stipules are well developed, and the leaves are relatively small and stiff in comparison to other species of *Carapichea* as well as generally obtuse at the apex, an unusual condition in this genus.

20. Carapichea tillettii (Steyerm.) C. M. Taylor, comb. nov. Basionym: *Psychotria tillettii* Steyerm., Mem. New York Bot. Gard. 23: 496, fig. 70. 1972. TYPE: Guyana. Upper Mazaruni River Basin, in low forest near former village of Suru-a-gu-puh, at head of Suru-a-gu-puh River, 470 m, 12 Sep. 1960, *S. S. Tillett & C. L. Tillett 43946* (holotype, NY[00132844], NY digital image!).

This species is known from escarpment forest at elevations of 1070–1570 m in the highlands of Guyana. The protologue described this species as having opposite leaves but the leaf arrangement actually varies, with plants from Merume Mountain having opposite leaves, those from Mt. Wokomong having verticillate leaves, and plants from Mt. Ayanganna variable in this regard with one specimen from this last area (*D. Clarke et al. 9062*, MO) having both conditions on one stem.

VI. *Stachyococcus* Group

This group comprises two species found in lowland wet vegetation at elevations of 100–300 m in the western Amazon basin. These species share a green drying color, relatively small stipules, inflorescences with reduced bracts and the flowers arranged in dense glomerules or heads, and relatively large fruits. The leaves lack acarodomatia. The leaves of *Carapichea adinantha* have well-developed secondary veins and also several short intersecondary veins between each pair of secondary veins, and the higher-order venation is sometimes visible or sometimes not visible; the leaves of *C. verrucosa* have the secondary veins hardly visible and the remaining venation not visible. The corollas of *C. adinantha* are white with well-developed adaxial projections on the lobes, and the anthers and stigmas are both included and situated in the lower part of the corolla tube; its floral biology is unknown, but if these flowers are distylous they have an unusual arrangement. The flowers of *C. verrucosa* are unknown. The fruits of these two species are reported to be spongy and variously blue, violet, purple, yellow, brownish yellow, or white. The pyrenes of both species are relatively large and thin-walled; those of *C. verrucosa* are abaxially verrucose, a unique feature within the genus and perhaps in the Neotropical Psychotrieae and Palicoureeae.

21. Carapichea adinantha (Standl.) C. M. Taylor, comb. nov. Basionym: *Retiniphyllum adinanthum* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8(5): 355. 1931. *Stachyococcus adinanthus* (Standl.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(6): 144. 1936. TYPE: Peru. Loreto: in clearing, Mishuyacu, near Iquitos, 100 m, Feb.–Mar. 1930, *G. Klug 988* (holotype, F-612612!; isotypes, NY[00133128], NY digital image!, US-1455972, US digital image!).

This species is known from wet forests on terra firme at elevations of ca. 100–200 m in Amazonian Peru, Colombia, and western Brazil. A description was presented by Taylor (1997: 636; as *Stachyococcus adinanthus*). This species is unusual in its spiciform inflorescences, corollas that are granular-puberulous on the external surfaces, and relatively large fruits with smooth, thin-walled pyrenes. The fruits are usually described as blue, violet, or purple, but one collector reported them to be white (*R. Vásquez & Soto 11870*, MO!) and another as black (*R. Vásquez & N. Jaramillo 10125*, MO!).

22. Carapichea verrucosa C. M. Taylor, sp. nov. TYPE: Peru. Loreto: prov. Maynas, distr. Punchana, Río Momón, trocha del caserio de San Antonio, en terreno alto, monte abierto y arcilloso, c. 120 m, 23 July 1998, *M. Rimachi Y.*

12346 (holotype, USM-185437!; isotype, MO-04904145!). Figure 2.

Haec species a congeneris inflorescentia capitata bracteis parvis, fructu satis grandi spongioso verrucoso albo usque brunneolo-flavido atque pyrenis abaxialiter verruculosis distinguitur.

Shrubs or trees, flowering at 1.5 m tall, to 8 m tall, somewhat fleshy, drying green to brown; stems subterete to subquadrate, glabrous. Leaves opposite; blades elliptic to elliptic-oblong, 10–26 × 2.6–9.8 cm, drying chartaceous, glabrous on both surfaces, at base acute to cuneate, at apex acuminate with tips 0.8–2.5 cm and often curved; secondary veins 5 to 8 pairs, usually looping to interconnect at least in basal part of blade, weakly visible, remaining venation not visible, adaxially with midrib plane to thinly prominulous and remaining venation plane, abaxially with midrib thinly prominent, secondary veins prominulous to plane, and remaining venation plane; petioles 10–27 mm; stipules interpetiolar, narrowly triangular to lanceolate or ligulate, 6–15 × 3–6 mm, obtuse to acute or sometimes weakly erose, glabrous, becoming dry, brown, and stiffly papery to somewhat indurated from apex downward, fragmenting with age, usually leaving an irregular, persistent basal portion. Inflorescences terminal, capitate to subcapitate or shortly spiciform; peduncle 0.8–2 cm, puberulous, flattened; heads (not including fruits) 1–2 × 1–1.2 cm, 15- to 30-flowered; bracts broadly triangular to rounded, 0.8–1.2 mm, glabrous, subtending several outermost flowers of groups. Flowers (postanthesis) sessile or subsessile; ovary portion obconic, ca. 1 mm, glabrous; calyx limb 1–1.2 mm, truncate to sinuate or shallowly, irregularly lobed, glabrous; corolla, anthers, and stigmas not seen. Fruits ellipsoid, yellow, brownish yellow, or creamy white, 2.5–3 × 2–2.5 mm, spongy, with thickened ring at apex, covered with low warty or scabrous growths or points; pyrenes 2, planoconvex, bony, abaxially smooth except weakly verrucose, adaxially smooth with raphal plug and thin median furrow that connects at apex to 2 marginal furrows, dehiscent through raphal plug and adaxial furrow.

Habitat, distribution, and phenology. This species is known from wet, noninundated forests at elevations of 100–300 m in the northwestern Amazonian basin of Brazil, Colombia, and Peru; it has been collected with fruits in April, June, July, and November.

IUCN Red List category. *Carapichea verrucosa* does not meet the geographic range criteria for any threatened category in its extent of occurrence (EOO) but meets the criterion for Endangered in its limited AOO based on the widely scattered collection localities. This species is known from six localities (i.e., different threat regimes) and is found in two different legally protected areas in two countries across a linear geographic range of 1200 km. It is apparently not common locally, but it is widespread. It is here assessed as Least Concern (LC).

Notes. This new species is notable for its relatively large, spongy, creamy white, yellow, or yellowish brown fruits with a finely warty exterior and a thickened ring at the apex and for its pyrenes that are verruculose on the abaxial surface; the specific epithet refers to the warty surfaces of the fruits and pyrenes.

Paratypes. BRAZIL. **Acre:** Sena Madureira, Faz. São Jorge I, BR-364 Km. 107, ramal de Toco Preto, 9°26′S, 68°37′W, *H. Medeiros, C. C. Berg, W. Castro, E. C. Oliveira, F. A. Obermuller & M. Silveira 476* (MO). COLOMBIA. **Amazonas:** correg. Araracuara, Parcela No. 16, 0°56′S, 71°47′W, *A. Duque, A. M. Benavides, A. León, A. Matapi "y otros" 8061* (COAH); mpio. Leticia, correg. Tarapacá, Parque Nac. Nat. Amacayacu, Cabaña Loreno (Río Cotuhé), *A. Rudas, P. Palacios, S. Duque, F. del Aguilar Joaquín & G. Morán 2427* (COL, MO). PERU. **Loreto:** prov. Loreto, Nauta, Río Marañón, *R. Vásquez & N. Jaramillo 3431* (AMAZ, MO, USM). **Ucayali:** E of Aguaytia, betw. Pucallpa Rd. & Río Aguaytia, *M. E. Mathias & D. Taylor 5015* (MO, USM).

VII. Bahia Group

This group comprises one species found in lowland Atlantic forests in eastern Brazil. This species is unusual in *Carapichea* for its deeply bilobed stipules with very narrow lobes, but the stipules are similar to those of other species in this genus in becoming marcescent and then fragmenting and falling off before the leaves, and some other species of *Carapichea* also have bilobed stipules (e.g., *C. guianensis*, *C. tillettii*). The leaves lack acarodomatia, and have few visible intersecondary veins with the higher-order venation usually not visible. The floral biology of this species is unknown, but the flowers described in the protologue are similar to the short-styled form of distylous species. The fruits are described as deep purple.

23. Carapichea lucida J. G. Jardim & Zappi, Kew Bull. 63(4): 661, fig. 1. 2008. TYPE: Brazil. Bahia: Elísio Medrado, ca. 1 km Monte Cruzeiro, Reserva Particular Jequitibá, Serra da Jibóia, 12°52′S, 39°28′W, 600–650 m, 1 Dec. 2004, *J.[G.] Jardim et al. 4280* (holotype, HUEFS not seen; isotype, CEPEC not seen).

This species is found in Atlantic forests at elevations of 200–800 m in Bahia State in eastern

Brazil. It is distinctive in *Carapichea* for the combination of its stipules with two well-developed narrow lobes and its capitate inflorescences with large, shiny, bright green bracts. A description and illustration were presented by Jardim and Zappi (2008). This is the only species of *Carapichea* so far known from eastern Brazil. The additional collectors of the type specimen are not listed in the protologue.

Excluded Name

Carapichea patrisii DC., Prodr. 4: 536. 1830. *Cephaelis patrisii* (DC.) D. Dietr., Syn. Pl. 1: 773. 1839. *Uragoga carapichea* Kuntze, Revis. Gen. Pl. 2: 955. 1891, non *Uragoga patrisii* (DC.) Kuntze, 1891. TYPE: French Guiana. S. loc., *Patris s.n.* (holotype, G-DC not seen; isotype, G!). [= *Psychotria hoffmannseggiana* (Willd. ex Roem. & Schult.) Müll. Arg. (Steyermark, 1972)].

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Appendix 1. Alphabetical List of Accepted Species

The number following a plant name indicates the order of treatment in this article. Additional information including synonymy can be found in this article and also in the TROPICOS online database.

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C. altsonii (Sandwith) C. M. Taylor, 15
C. araguariensis (Steyerm.) C. M. Taylor, 9
C. crebrinervia (Standl.) C. M. Taylor, 10
C. dolichophylla (Standl.) C. M. Taylor, 3
C. fimbriflora (Steyerm.) C. M. Taylor, 11
C. franquevilleana (Müll. Arg.) C. M. Taylor, 4
C. guianensis Aubl., 5
C. ipecacuanha (Brot.) L. Andersson, 1
C. klugii (Standl.) C. M. Taylor, 6
C. ligularis (Rudge) Delprete, 12
C. lucida J. G. Jardim & Zappi, 23
C. maturacensis (Steyerm.) C. M. Taylor, 7
C. necopinata (Standl.) C. M. Taylor, 13
C. nivea (Sandwith) C. M. Taylor, 16
C. pacimonica (Müll. Arg.) C. M. Taylor, 14
C. panurensis (Müll. Arg.) C. M. Taylor, 19
C. sandwithiana (Steyerm.) C. M. Taylor, 17
C. tillettii (Steyerm.) C. M. Taylor, 20
C. urniformis (Steyerm.) C. M. Taylor, 18
C. vasivensis (Müll. Arg.) C. M. Taylor, 8
C. verrucosa C. M. Taylor, 22

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Cover illustration. ***Siculosciadium nebrodense*** **(Guss.) C. Brullo, Brullo, S. R. Downie & Giusso, drawn by Salvatore Brullo.**

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The mission of the Missouri Botanical Garden is to discover and share knowledge about plants and their environment, in order to preserve and enrich life.

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REPORT OF THE SECOND CONFERENCE AND GENERAL MEETING OF THE GLOBAL PARTNERSHIP FOR PLANT CONSERVATION[1]

Peter Wyse Jackson[2]

ABSTRACT

The second conference of the Global Partnership for Plant Conservation (GPPC) was organized by the GPPC, in association with the Secretariat of the Convention on Biological Diversity (SCBD) and Botanic Gardens Conservation International (BGCI). This general meeting was hosted by the Missouri Botanical Garden and was held 5–7 July 2011, in St. Louis, Missouri.

Key words: Convention on Biological Diversity (CBD), Global Partnership for Plant Conservation (GPPC), Global Strategy for Plant Conservation (GSPC).

At its sixth meeting, the Conference of the Parties (COP) to the Convention on Biological Diversity (CBD, 2002) adopted Decision VI/9 on the Global Strategy for Plant Conservation (GSPC), which included outcome-oriented global targets for 2010. The ultimate and long-term objective of the Strategy is to halt the current and continuing loss of plant diversity. The aim of the Strategy is to achieve plant conservation, and it is also concerned with aspects of sustainable use, capacity building, and benefit sharing.

The GSPC Expert Group meeting in Dingle, Co. Kerry, Ireland, in October 2003 noted that the Strategy provides a useful framework to bring together organizations and initiatives to meet common objectives and recommended the establishment of a wide global partnership to support its implementation (CBD, 2003).

The Global Partnership for Plant Conservation (GPPC) was subsequently launched on 13 February 2004 at a meeting held during the seventh COP of the CBD, in Kuala Lumpur, Malaysia. In its Decision VII/10 on the GSPC (CBD, 2004), the COP welcomed the establishment of the GPPC and encouraged the participating organizations to continue to contribute to the implementation of the Strategy. It also invited other organizations to join the Partnership and encouraged Botanic Gardens Conservation International (BGCI) to continue its support for the Partnership.

The aim of the Partnership is to support the worldwide implementation of the GSPC, and its objective is to provide a framework to facilitate harmony between existing initiatives aimed at plant conservation, identify gaps where new initiatives are required, and promote mobilization of the necessary resources.

[1] This and the following 13 articles are the proceedings of the Global Partnership for Plant Conservation Conference, "Supporting the Worldwide Implementation of the Global Strategy for Plant Conservation." The conference was held 5–7 July 2011, at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

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The Partnership also brings together a diversity of groups working in different areas for plant conservation, such as protected areas, species, botanic gardens, agricultural biodiversity, forestry, wetlands, etc.

The COP further welcomed the establishment, by the Executive Secretary, of a flexible coordination mechanism for the Strategy, comprising: liaison groups to be convened as necessary according to established procedures; national focal points, as determined by Parties; the GPPC; and the Secretariat, including the Programme Officer supported by BGCI. It encouraged Parties to nominate focal points, or designate from among existing focal points, for the Strategy in order to promote and facilitate implementation and monitoring of the Strategy at a national level; promote the participation of national stakeholders in the implementation and monitoring of the Strategy at a national level; and facilitate communication among national stakeholders and the Secretariat and GPPC.

In October 2010 in Nagoya, Japan, the 10th Conference of the Parties (COP 10) to the CBD adopted the Updated GSPC 2011–2020 by Decision X/17 (CBD, 2011a). This decision incorporated a consolidated update of the GSPC for the period 2011–2020. This updated GSPC includes 16 targets for plant conservation (CBD, 2011b) to be achieved by 2020 and invites Parties and other governments to develop or update national and regional targets as appropriate and, where appropriate, to incorporate them into relevant plans, programs, and initiatives, including national biodiversity strategies and action plans, and to align the further implementation of the Strategy with national and/or regional efforts to implement the Strategic Plan for Biodiversity 2011–2020 (CBD, 2011c).

The first Conference of the GPPC was held in Dublin, Ireland, in October 2005. Working practices for the GPPC were adopted by the GPPC (2005) at its first general meeting held in conjunction with this conference on 25 October 2005 in Dublin.

Introduction

The second conference of the GPPC was held from 5–7 July 2011 in St. Louis, Missouri. The second General Meeting of the GPPC was also held in conjunction with this conference on 7 July 2011. The conference was followed by a meeting of the GSPC Liaison Group, with their report through the CBD (2011d).

The 2011 conference was organized by the GPPC in association with the Secretariat of the Convention on Biological Diversity (SCBD) and BGCI; it was hosted by the Missouri Botanical Garden. The conference provided information through plenary sessions and strategic discussions to guide future plant conservation priorities in national development agendas with links to the implementation of the CBD's Strategic Plan, as well as providing guidance for countries that are updating national biodiversity strategies. The meeting was designed to showcase examples and share experience from around the world on GSPC implementation, particularly during the period of 2002–2010, to provide guidance and support for national and regional GSPC implementation entering into the new phase; to assist the ongoing efforts to consider and develop further the technical rationales, milestones, and indicators for the GSPC up to 2020; and to harmonize with the Strategic Plan for Biodiversity 2011–2020 (CBD, 2011e). A key objective of the conference was also to showcase and discuss a draft Toolkit for GSPC implementation.

The conference brought together plant conservation scientists, policymakers, and practitioners representing 27 countries from throughout the world to share methods and results to advance plant conservation measurably. The conference delegates shared their experiences and furthered the development of plant conservation science in the United Nations Decade of Biological Diversity (<www.cbd.int/2011–2020/>).

Opening, Discussions, and Progress

The conference opened with Dr. Peter Wyse Jackson, President of the Missouri Botanical Garden and Chairman of the GPPC, welcoming delegates to St. Louis. He noted with pleasure how many organizations and institutions active in plant conservation around the world were represented at the meeting. He also acknowledged the presence at the conference of Dr. Peter H. Raven, former President of the Missouri Botanical Garden, whose original call for the development of a global initiative for plant conservation to be developed through the United Nations had led to a resolution from the XVIth International Botanical Congress (IBC) in 1999 in St. Louis, Missouri, calling for such a program. Following this IBC, this had been taken forward by a group of botanists at a meeting in Gran Canaria, Spain, who developed an outline of what was later developed and adopted by the United Nation's CBD in April 2002. Dr. Wyse Jackson also recognized Dr. David Bramwell, Director of the Jardín Botánico Canario, Viera y Clavijo, Las Palmas de Gran Canaria, Spain, who had hosted the landmark Gran Canaria meeting in 2000.

Dr. Wyse Jackson thanked the members of the GPPC for their work in support of the GSPC since the Partnership had been established in 2004 (CBD, 2004). He noted that many members of the Partnership were represented at the conference and thanked participants for having traveled to St. Louis from so many countries to attend this meeting, an important landmark in the development and imple-

mentation of the GSPC, now entering its second phase following the adoption of the updated Strategy at the COP 10 to the CBD in Nagoya, Japan, in October 2010.

He noted that the outcomes of the conference would be communicated to and discussed by participants attending the fourth GSPC Liaison Group meeting that would be held also in St. Louis following the conference of 8–9 July (cf. CBD, 2011d). The conference, therefore, presented an important opportunity for many plant conservation practitioners, botanists, and policymakers to ensure that their concerns are communicated to the CBD's Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA), which would receive the Liaison Group's report and recommendations.

Ms. Sara Oldfield, Secretary General of BGCI, welcomed delegates on behalf of BGCI and thanked the Missouri Botanical Garden for hosting the conference. She pointed out the significant responsibilities of the conference to help determine priorities and new effective actions in order to achieve the GSPC targets.

Mr. Robert Höft, Environmental Affairs Officer at the SCBD, also welcomed delegates on behalf of Dr. Ahmed Djoghlaf and read a statement on his behalf (<http://www.cbd.int/doc/speech/2011/sp-2011-07-05-gppc-en.pdf>). In his remarks, Mr. Höft challenged the participants to consider the ways in which the GSPC could be made more relevant to and prominent in political processes worldwide, particularly at national levels, suggesting that only when plant conservation is effectively integrated into programs for sustainable economic development and poverty alleviation will its objectives be fully achieved. He pointed out the need for close operational links to be ensured between the GSPC and the Strategic Plan for Biodiversity, also adopted by the CBD in October 2010 in Nagoya.

St. Louis Public Radio, part of the National Public Radio network, had a special broadcast recorded live from the conference (<http://www.stlpublicradio.org/programs/slota/archivedetail.php?date='2011-07-06/>). Discussion was about The Future of Plant Conservation between the moderator and four panelists; the moderator took questions from the audience.

The 2011 GPPC Conference included six plenary sessions and eight workshops. Plenary sessions included: (1) the GSPC 2010–2020; (2) understanding and documenting plant diversity; (3) conserving plant diversity; (4) ecological restoration and the GSPC; (5) using plant diversity sustainably; and (6) building capacity for plant conservation. Workshop outcomes and recommendations are discussed below.

GPPC Workshop No. 1: The World Flora: Possibilities and Perspectives—A Stakeholder Consultation

(1) Major assets to complete a World Flora by 2020 include existing data and frameworks: (a) The Plant List to define the list of species to include in the World Flora; (b) more than 250 years of published floras, treatments, and monographs; and (c) the Angiosperm Phylogeny Group APG3 classification system (Stevens, 2001 onward) to define family-level framework.

(2) A major constraint for the GSPC Target 1, "an online flora of all known plants" (CBD, 2011b), is the 2020 deadline for delivery. Attendees acknowledged that achieving 100% completeness may be impossible, but believe that 80% completeness with 100% confidence in product could possibly be achieved. They also agreed that the project must leverage existing floras and datasets and do new fieldwork and taxonomic research only where data gaps occur.

(3) The World Flora should include a minimum set of required fields while maintaining high-quality, trustworthy data. The content should be defined by a working group who will take under consideration the audience for the project.

(4) Human capacity building is a key activity in delivering the World Flora, as the project has the potential to engage hundreds, if not thousands, of taxonomists, parataxonomists, students, and citizen scientists from all over the world. It is important to consider the human resources needed to execute the project as well as the resources needed post-2020.

(5) Building networks will be a key factor to achieve the GSPC Target 1, and participating institutions should work in areas of the world where they have regional or monographic focus.

(6) Tools for collaborative work should be developed, such as an interactive web site and application programming interfaces for data use.

GPPC Workshop No. 2: The GSPC Toolkit—A Discussion Workshop

(1) The GSPC Toolkit (CBD, 2013) should include clear links to the CBD Strategic Plan Targets (CBD, 2011b) and to show the relevance of the GSPC in the context of national biodiversity strategies. Also included is basic information to explain why individual countries need to develop implementation strategies.

(2) The GSPC Toolkit should encourage individual organizations to take responsibility for specific GSPC targets and to help with peer review and quality control.

(3) The GSPC Toolkit should provide different entry points for different users to help them navigate more efficiently around the site.

(4) Off-line access is important; therefore, the GSPC Toolkit should consider generating a series of short publications that would be practical to produce and to update. Although a wiki-based approach and smart-phone accessibility are not taken initially, these should be considered in the longer term.

(5) Stakeholders could help to translate materials that are useful to make them available in different languages, although most resources should be made available in the language in which they are prepared.

GPPC WORKSHOP NO. 3: RED LISTING AND ACHIEVING THE GSPC TARGET 2

(1) Much greater progress toward achieving the GSPC Target 2, "an assessment of the conservation status of all known plant species, as far as possible, to guide conservation action" (CBD, 2011b), has been made than is currently realized, i.e., as perceived only through the lens of the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (IUCN, 2001, 2012), which includes just 17,604 plant species, or still only 5.7% of the estimated total. In fact, well over 100,000 plant species (Wyse Jackson, pers. obs.) have been assessed at either the global or national level for their conservation status in the past 25 years, many using the IUCN Red List Categories and Criteria, but also many others using different assessment systems. There is an urgent need to record and synthesize all of these assessments in an accessible online database to better inform conservation actions.

(2) Assessors should be strongly encouraged to use the IUCN Red List Categories and Criteria (IUCN, 2001, 2012) for future assessments. However, in order to expedite the incorporation of assessments on to the IUCN Red List of Threatened Species, it is suggested that IUCN should further review, revise, and clarify the minimum documentation standards required for inclusion on the Red List.

(3) Assessors should be strongly encouraged to use the IUCN Red List Categories and Criteria (IUCN, 2001, 2012) for future assessments. However, in order to expedite the incorporation of assessments within the IUCN Red List of Threatened Species, it is suggested that the IUCN should further review, revise, and clarify the minimum documentation standards required for inclusion on to the Red List.

(4) For the majority of plant species that are most likely of lesser conservation concern, more rapid assessment of their nonthreatened status can and should be achieved.

(5) The online World Flora (GSPC Target 1, CBD, 2011b) is the most appropriate place to attach and/or link conservation assessments of all plant species. Therefore, as the development of the World Flora moves forward, it is essential that considerations on how to link to existing online databases of conservation status, e.g., IUCN Red List or NatureServe (National Biological Information Infrastructure [NBII], 2013), as well as how to incorporate assessments that are not online, be addressed.

GPPC WORKSHOP NO. 4: ECOLOGICAL RESTORATION AND THE GSPC

(1) Follow The Economics of Ecosystems and Biodiversity (TEEB, 2013; e.g., Wittmer et al., 2013) strategy of producing documents to explain the GSPC for five audiences: (a) scientists and professionals, (b) national and international policymakers, (c) corporate leaders and decision makers, (d) local and regional administrators, and (e) private consumers and citizens.

(2) Develop a framework to summarize, assess, promote, and multiply broad, integrated plant conservation and ecological restoration efforts that contribute to achieving the GSPC targets (CBD, 2011b). A summary of current efforts is needed to engage organizations, corporations, and institutions, and to help leverage resources for additional efforts and collaborations.

(3) Promote and link the long-standing efforts of the Society for Ecological Restoration, the GPPC, and others. Develop, document, and expand an international network of Long-term Ecological Restoration (LTER) areas (LTER Network, 2013). Encourage links with the work of the World Commission on Protected Areas (WCPA) in the area of ecological restoration (IUCN, 2013).

(4) The tools developed for implementing the GSPC targets and for achieving the GSPC Objectives (CBD, 2011b) should encourage and promote the use of the terms ecological restoration and Restoring Natural Capital (RNC), as used by TEEB and the RNC Network (Aronson et al., 2013).

GPPC WORKSHOP NO. 5: TECHNICAL RATIONALES, MILESTONES FOR THE GSPC TARGETS—LINKING WITH THE CBD STRATEGIC PLAN

(1) The GSPC Technical Rationales (CBD, 2011e) are very useful to practitioners in explaining the GSPC targets to other stakeholders, including donors and policymakers in particular, as they explain the importance of the individual targets while also showing how the 16 targets link together into a plan.

(2) The GSPC Technical Rationales help users to define indicators and identify relevant stakeholders.

(3) These Technical Rationales should include explicit links to the CBD Strategic Plan (CBD, 2011c, 2011e). They should also provide the entry point for more detailed information as would be available, e.g., from the GSPC Toolkit.

(4) Technical Rationales should be kept brief and should be included in key materials about the GSPC (brochures and posters).

(5) Technical Rationales need to be made available as soon as possible in all the official languages of the CBD.

(6) If possible, GSPC Technical Rationales should include information on progress to date, suggested milestones, and indicators of success.

GPPC WORKSHOP NO. 6: LINKING THE GSPC AT AN INSTITUTIONAL LEVEL—A DISCUSSION WORKSHOP

(1) Insofar as possible, institutions should use the GSPC Objectives (CBD, 2011b) as a guide to help recognize their strengths and the work they are already doing in the conservation arena.

(2) Institutions should also use, as possible, the GSPC as a framework to build on these strengths and to set institutional priorities for the future, with the understanding that individual institutions need not necessarily address each GSPC target (CBD, 2011b).

(3) Institutions should make special efforts to work with their government representatives to raise awareness of and enlist support for advancing the GSPC.

(4) Institutions should use, as they can, the GSPC as a framework to integrate programs across the institution.

(5) Institutions should request that the SCBD invite the Parties to comply with the decision they have adopted to include the GSPC as part of their commitment to the CBD. They should also encourage the Parties to include the GSPC targets in their national biodiversity strategies and action plans.

(6) Institutions should develop networks, partnerships, or other types of institutional collaborations adapted to the particular situation of each country and capable of carrying out work in plant conservation to help realize the GSPC targets. To implement these collaborations, it will be important to find ways to identify and support individuals who will spur the formation of these collaborations.

GPPC WORKSHOP NO. 7: THE GSPC, ACCESS AND BENEFIT-SHARING, AND THE NAGOYA PROTOCOL

(1) The GPPC and individual organizations could provide educational opportunities around the operations and the documentation necessary for compliance and best practices in plant conservation. The GPPC could also play a role, through the member organizations, in the education of decision makers.

(2) The GPPC could play a greater role in representing the plant conservation community at meetings of Parties and negotiations. In addition, individual organizations should monitor and lobby to ensure that national laws remain open to scientific exchange of material.

(3) With regard to Article 10 ("Global Multilateral Benefit-Sharing Mechanism") and Article 11 ("Transboundary Cooperation") of the Nagoya Protocol (CBD, 2011f), the GPPC could play an important role in advocating for simplification to make securing prior informed consent easier.

(4) There is a need to focus efforts on the opportunities presented by the Access and Benefit-sharing (ABS) framework (CBD, 2011g), rather than on the challenges of obtaining genetic material.

(5) Benefits should be outlined from existing projects to provide a context for negotiation toward securing genetic material. It would be important to develop case studies, in particular cases that illustrate work conducted by those countries with large plant diversity that can provide guidance to others on maintaining open exchange of genetic material, as examples to help decision makers.

(6) Institutions should be more cognizant as a group not to make mistakes with negotiations and in the handling of plant material. In recognizing that a single institution can have a wider effect on the way in which institutions from an entire country could be viewed, the GPPC and individual institutions could help in raising awareness and providing support.

GPPC WORKSHOP NO. 8: PUBLIC AWARENESS AND THE GSPC

(1) The workshop focused primarily on the role of botanic gardens in public awareness on plant conservation and the GSPC. If botanic gardens are already collectively playing host to 250 million visitors a year, they should invest in ensuring that those 250 million visitors have an enriching, enlightening, and inspiring experience as possible.

(2) Botanic gardens should personalize learning opportunities and give people the opportunity to connect with the message in ways relevant to them. To make bigger impacts in the communities that they serve, botanical gardens should focus their message on targeted audiences and on specific groups whose decisions and actions can have long-term, significant conservation impacts.

(3) Botanic gardens should mobilize themselves in a way that leverages their collective reach. For example, if botanical gardens had e-mail addresses

for all 250 million visitors worldwide in one massive e-mail list, these institutions, through perhaps BGCI, could communicate and share discussions with patrons and visitors in entirely new ways.

(4) Botanic gardens should create a global campaign. With the diversity of media channels available today (social and traditional), botanic gardens should mount and disseminate a global campaign focused on the role of plants in human life.

Business Meeting

The meeting was opened by Dr. Wyse Jackson, Chair of the GPPC. Ms. Suzanne Sharrock (BGCI and GPPC Secretariat) acted as rapporteur for the meeting. The agenda for the meeting was as follows: (a) future priorities and role, (b) structure and membership, (c) election of officers, and (d) other business.

(a) future priorities and role

Discussion noted that various options exist for the future role of the GPPC by (a) maintaining the status quo, (b) developing a specific work program, (c) playing a direct role in supporting the development of the GSPC Toolkit, (d) focusing on communications, and (e) the sharing of resources between members. It was recommended that the presentations made during the GPPC Conference should be made publically available. It was also noted that Missouri Botanical Garden was considering publishing the proceedings of the conference in an issue of the *Annals of the Missouri Botanical Garden*.

Discussion pursued that the GPPC could play an important role in providing resources and advising and facilitating with the GSPC Toolkit. The issue of facilitating agencies for each GSPC target was discussed. It was believed that a wider number of institutions should now be engaged around each target and that among other tasks (e.g., monitoring and reporting on implementation progress), they should have a specific focus on supporting toolkit development. It was, therefore, recommended that the GPPC should establish a series of working groups, which would focus either on specific targets of the GSPC or on the broader objectives of the GSPC. The plans and objectives of these working groups would be developed by the GPPC Chair and circulated among the membership, together with a request for members to participate in the working groups. It was suggested that each working group should nominate a Chair who would act as the main liaison between the working group, the GPPC Chair, and the GSPC Toolkit administrator.

It was agreed that the document Working Practices of the GPPC should be revised and updated within the 2020 framework. The Chair of the GPPC will circulate this document to members, requesting comments and suggestions for updates. The updated draft of this document is included in Annex 1. This draft includes the modalities for the proposed GPPC working groups.

(b) structure and membership

Following discussion on the size of membership of the Partnership, it was agreed that structure and membership should be allowed to evolve naturally, with consideration given to increasing the scope and area of expertise of the members, e.g., by encouraging greater participation from the agriculture and forestry sectors.

(c) election of officers

The business meetings of the GPPC provide the opportunity for the GPPC Chair and Secretariat to be elected. Because there were no new nominations for either of these positions, it was agreed that Dr. Wyse Jackson would continue as Chair of the GPPC, and BGCI would continue to provide the secretariat until the next general meeting of the partnership.

(d) other business

The question of support for the GPPC Chair was raised, noting that up to now support has been informal, but the GSPC Liaison Group has played a role. With the formation of GPPC working groups, the Chairs of the working groups would be able to support the GPPC Chair. Dr. Wyse Jackson informed that he would look for additional institutional support from among the membership, including the Missouri Botanical Garden, where the office of the GPPC Chair would be maintained.

Following the completion of the General Meeting the conference was closed.

Conference Attendees and Program

A list of the GPPC Conference participants is provided at <https://mbgserv18.mobot.org/ocs/index.php/gppc/gppcstl/about/editorialPolicies#custom-0>.

The conference program and schedule, including the abstracts of presentations, are respectively provided at <https://mbgserv18.mobot.org/ocs/index.php/gppc/gppcstl/schedConf/program> and <https://mbgserv18.mobot.org/ocs/index.php/gppc/gppcstl/schedConf/schedule>.

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Annex 1. Updated Working Practices of the GPPC. The annex can be accessed at <http://www.plants2020.net/gppcworking-practices/>.

Introduction

1. The GPPC brings together international, regional, and national organizations in order to contribute to the implementation of the GSPC of the CBD. The Partnership aims to support the GSPC. The inaugural meeting of the Partnership was held as a side event of the seventh meeting of the

Conference of the Parties of the Convention in Kuala Lumpur in February 2004. The Conference of the Parties welcomed the establishment of the Partnership.

2. This note outlines the establishment of the Partnership and its Working Practices in relation to its aims, membership, functions, working modalities, chairmanship and secretariat, meetings and reporting.

3. Originally adopted by the GPPC at its first general meeting held in Dublin, Ireland, on 25 October 2005, this draft includes possible updates and revisions to be considered by the GPPC membership in response to the adoption by the CBD of an updated GSPC in November 2010 and the incorporation of GSPC targets for 2020.

4. It is noted that nothing in this Working Practices document should be read to contradict the principles of the CBD. Furthermore, it is recognized and accepted that this document is not legally binding and will have no effect as a legal or political precedent.

Establishment

5. At its sixth meeting, the Conference of the Parties to the CBD adopted Decision VI/9 on the GSPC, which includes outcome-oriented global targets for 2010. The ultimate and long-term objective of the Strategy is to halt the current and continuing loss of plant diversity. While the entry point for the Strategy is plant conservation, it is also concerned with aspects of sustainable use, capacity building, and benefit-sharing.

6. The GSPC Expert Group meeting in Dingle, Co. Kerry, Ireland, in October 2003 noted that "the Strategy is providing a useful framework to bring together organizations and initiatives to meet common objectives. Various organizations are already working towards the respective targets, and where possible, they are incorporating actions towards achieving targets into existing work programs. The need for wider partnerships has been noted, and to achieve this, mechanisms by which a wider group of organizations could be involved in the process are needed, with the emphasis being given to a partnership approach within the Strategy as a whole, rather than a specific target-related involvement" (CBD, 2003: 7; UNEP/CBD/SBSTTA/9/INF/24). The GSPC Expert Group, therefore, recommended that a global partnership for plant conservation be established, building upon the Gran Canaria Group, an informal consortium of international and national organizations that came together in 2000 to support the development of a global strategy for plant conservation. The Expert Group further proposed that a global partnership for plant conservation be open to all organizations that can contribute to the implementation of the Strategy.

7. In February 2004, in its Decision VII/10 on the GSPC, the Conference of the Parties welcomed the establishment of the Global Partnership for Plant Conservation and encouraged the participating organizations to continue to contribute to the implementation of the Strategy. It also invited other organizations to join the Partnership and encouraged BGCI to continue its support for the Partnership.

8. The Conference of the Parties further welcomed the establishment, by the Executive Secretary, of a flexible coordination mechanism for the Strategy, comprising: liaison groups to be convened as necessary according to established procedures; national focal points, as determined by Parties; the GPPC; and the Secretariat, including the Programme Officer supported by BGCI. It encouraged Parties to nominate focal points, or designate from among existing focal points, for the Strategy in order to promote and facilitate implementation and monitoring of the Strategy at a national level; promote the participation of national stakeholders in the implementation and monitoring of the Strategy at national level; and facilitate communication between national stakeholders and the Secretariat and GPPC.

9. The Partnership launched at an event held on 13 February 2004 during the 7th Meeting of the Conferences of Parties to the CBD in Kuala Lumpur, Malaysia. The establishment of the Partnership was welcomed by the CBD Executive Secretary and by representatives of a range of national and international organizations.

Aim of the Partnership

10. The aim of the Partnership is to support the worldwide implementation of the GSPC and its objective to provide a framework to facilitate harmony between existing initiatives aimed at plant conservation, identify gaps where new initiatives are required, and promote mobilization of the necessary resources. The Partnership also brings together a diversity of groups working in different areas for plant conservation, such as protected areas, species, botanic gardens, agricultural biodiversity, forestry, wetlands, etc.

Working Modalities

11. The Partnership represents a voluntary commitment by participating organizations to a common cause, the GSPC, who have agreed to come together in the framework of a GPPC to support the GSPC implementation. Furthermore, it is recognized that the Partnership does not seek to compromise the independence of any of its participating organizations but aims to create synergies and add value to existing initiatives, particularly in support of national GSPC implementation and in supporting efforts being made by Parties in responding to the GSPC.

12. The Partnership recognizes and accepts that guidance in relation to the GSPC are set by the Conference of the Parties to the CBD and its subsidiary bodies. Further, it acknowledges its role in the flexible coordination mechanism of the GSPC. The activities of the Partnership will be consistent with guidance provided by the Conference of the Parties and its subsidiary bodies and take account of advice provided through the flexible coordination mechanism.

13. The Partnership may play a role in identifying gaps so that individual organizations and institutions may then take a lead in developing projects to help address those gaps within the broad, flexible framework provided by the Partnership, involving organizations both within and outside the Partnership as appropriate. The Partnership will seek to focus on enhancing projects and other activities that respond to the GSPC and support its implementation, particularly at national levels rather than endorsing specific projects.

14. The activities of the Partnership are outlined in a program of activities prepared and agreed on from time to time by the members.

15. An important role of the Partnership will be to enhance communication and collaboration between participating organizations. The priority will be to minimize duplication of effort and maximize on available limited resources and ensure clarity in communication such as in relation to approaches to donors.

16. Every effort will be made to ensure that the Partnership remains as flexible and non-bureaucratic as possible and able to adapt easily and respond to changing circumstances and opportunities.

17. Participating organizations of the Partnership will encourage cooperation among themselves in the implementation of the GSPC and the implementation of the programs of

activities of the Partnership in areas of mutual interest and with other appropriate bodies, to avoid duplication and to benefit from existing resources and expertise.

18. The approach of the Partnership will be: (a) to operate in an open, transparent and flexible manner; (b) to share information on policies, programs, and activities among its participating organizations; (c) to encourage active participation in the implementation of the GSPC and the program of activities of the Partnership at all levels; and (d) to hold regular meetings and ensure other communication among its participating organizations to consider and agree on its activities and ongoing arrangements.

Membership

19. The Partnership consists of organizations, institutions, secretariats, and other bodies that have substantial programs in plant conservation, all of which shall be eligible for membership.

20. Any bona fide organizations and institutions, including governmental and nongovernmental organizations (NGOs), indigenous peoples organizations (IPOs), and the private sector, that are playing an important role in supporting the implementation of the GSPC, are invited to participate in the Partnership. Membership is open to all bodies that endorse the objectives of the GPPC and are committed to facilitating and promoting its implementation, unless the participation of that organization in the Partnership would be likely to jeopardize the aims of the Partnership.

21. Organizations may become members by an exchange of letters between a responsible official of the organization and the Chair of the Partnership. The letter from the applying organization should endorse the GSPC and accept the aims and Working Practices of the Partnership.

22. The Chair will acknowledge the membership of the body joining the Partnership. The name of the new member will then be added to the list of members of the Partnership maintained on the Partnership web site (<www.plants2020.org>). If the bona fide nature of the application of the applicant organization is in doubt, the Chair may consult with the Vice Chairs, and if necessary with the other members of the Partnership, before accepting a membership application.

23. Organizations may withdraw from the Partnership by informing the Chair in writing of their withdrawal. Organizations may also be withdrawn from membership by the Partnership itself by an affirmative vote of a two-thirds majority of the members present and voting at a General Meeting.

Functions of the Partnership

24. The functions of the GPPC include: (a) to support the Executive Secretary of the CBD, the Parties, and the flexible coordination mechanism for the GSPC to implement the Strategy and help monitor progress in the achievement of the 16 outcome targets by 2020; (b) to promote the implementation of the GSPC through the activities and initiatives of its participating organizations, other partners, and associated networks; (c) to support the development of collaborative initiatives among its members in support of the achievement of the GSPC targets; (d) to support the development and implementation of national and regional strategies for plant conservation and strengthen integration of the elements and targets of the GSPC into sectoral and institutional programs and initiatives; (e) to stimulate, encourage, and support the development of national partnerships for plant conservation; (f) to assist in the development and dissemination of relevant models with protocols for plant conservation, best practices and case studies and provide relevant scientific and technical tools where available, for the implementation of the GSPC; (g) to participate in the flexible coordination mechanism of the GSPC as established by the CBD Executive Secretary; (h) to participate in the development and maintenance of a Toolkit on GSPC implementation; (i) to maintain a web site on the plant conservation activities of its members worldwide, as a resource for interaction and communication between initiatives and organizations active in plant conservation, working in close collaboration with the Clearing House Mechanism of the CBD; (j) to identify gaps where new initiatives are required; (k) to support capacity building initiatives for plant conservation especially in developing countries; (l) to facilitate education and public awareness on plant conservation and the GSPC; and (m) to maximize and mobilize existing and new resources to support the implementation of the Strategy at all levels.

Chair and Secretariat

25. A Chair for the Partnership is elected at the General Meetings of the Partnership.

26. Any changes to the arrangements for the Partnership will be agreed by the Partners and adopted at its General Meetings. A Secretariat for the Partnership shall be selected or designated also at General Meetings. The term of office of the Chair and any other officers chosen will be from one General Meeting to the next.

Meetings

27. The primary governing and decision-making body of the Partnership will be at its General Meetings. The General Meetings will be the means by which the participating organizations will make collective decisions on all matters relating to the GPPC, which will then be put into effect by the GPPC Secretariat. The Partnership's activities will be guided by the General Meetings. General Meetings will be held from time to time, if possible no less than once every three years, convened by the Chair. All members will be invited to be represented at a General Meeting. The General Meeting should strive to work by consensus whenever possible. If consensus cannot be reached after reasonable attempts have been made, then in exceptional circumstances a decision may be approved by a majority vote of those members present at a General Meeting. All members present at a General Meeting will be entitled to one vote.

28. The General Meetings may: (a) agree on the activities that will be undertaken by the Partnership for the period between General Meetings or for other agreed periods of time. The Partnership may, by consensus, make adjustments to these activities at any time; (b) agree on practices as may be required for the sound management of the Partnership's activities, while assuring adherence to this document and to the principles of the CBD and GSPC; (c) appoint a Chair and other officers and select or designate a Secretariat; (d) consider any matters pertaining to the GPPC or its operations and the GSPC as submitted to it by the Executive Secretary of the CBD, the GPPC Secretariat, or by any member; (e) establish Working Groups to support, advise on, and help monitor the achievement of individual or groups of targets of the GSPC and to contribute to and support, as appropriate, the development and maintenance of the GSPC Toolkit. General Meetings may be supplemented by occasional meetings held by teleconference and/or electronic communications.

Working Groups

29. The establishment of Working Groups to support, advise on, and help monitor the achievement of the GSPC 2020 targets was agreed at the second General Meeting of the Partnership.

30. A series of Working Groups are constituted for each of the first four GSPC Objectives, viz: (a) Objective I, plant diversity is well understood, documented and recognized; (b) Objective II, plant diversity is urgently and effectively conserved; (c) Objective III, plant diversity is used in a sustainable and equitable manner; and, (d) Objective IV, education and awareness about plant diversity, its role in sustainable livelihoods, and importance to all life on Earth is promoted.

TERMS OF REFERENCE FOR WORKING GROUPS

31. The terms of reference of Working Groups are as follows.

(a) Provide advice to the Executive Secretary to the CBD on, inter alia, the technical terms and rationale for each target. Such advice may be provided either directly to the Executive Secretary or as part of consultations undertaken at Liaison Group meeting, through the flexible coordination mechanism.

(b) Assist in the development and maintenance of the GSPC Toolkit, including: (i) help in identifying existing tools for inclusion; (ii) document case studies and information on best practices supporting the development of new plant conservation tools that may not currently exist to support GSPC implementation and to address identified gaps; (iii) develop and implement opportunities to disseminate the use of the Toolkit for the development of national and regional responses to the GSPC; and (iv) provide advice for the incorporation of the GSPC and its targets into national biodiversity strategies and action plans.

(c) Assist in monitoring progress toward the achievement of the GSPC 2020 targets, including any indicators and milestones identified and existing baselines.

(d) Identify capacity-building and networking needs for the achievement of the GSPC targets and support, encourage, advise on, and assist in the implementation of capacity-building measures at all levels.

(e) Promote a wider understanding and awareness of the GSPC and its targets for 2020 among the botanical, conservation, and broader environmental communities.

(f) Contribute toward updates of the Plant Conservation Report and periodic other reviews of the GSPC and its progress.

32. Additional cross-cutting Working Groups may be established as needed on a permanent or temporary basis by the GPPC membership to address particular topics, such as emerging issues, items of more general importance to the GSPC, or to consider matters for which the Executive Secretary has requested specific advice.

MEMBERSHIP AND PARTICIPATION IN WORKING GROUPS

33. Participation in these Working Groups is open to all members of the GPPC. Nevertheless, it is expected that organizations and institutions will participate primarily in the Working Groups where they have a direct interest and specific expertise and involvement.

34. Each Working Group will appoint a Chair and Secretary who will liaise directly with the membership of the Working Group to manage and organize the work of the Group. The Chair and Secretary will also liaise with and report to the GPPC Chair and Secretariat, with the aim of reporting on progress, activities, and outcomes of the work of the Group. The Chair and Secretary will be appointed by the membership of the Working Group and with the agreement of the GPPC Chair. Such appointments shall generally be by consensus. If an appointment cannot be made by consensus, then a Working Group Chair may be appointed by the GPPC Chair after consultation with the full GPPC membership.

35. Working Group Chairs may invite the participation of a limited number of technical advisors or experts as observers when they may be able to contribute information or perspectives on the work of the Group that might not otherwise be available to it from within the membership of the GPPC.

36. It is expected that where a GPPC member wishes to be involved in a specific Working Group, the member will nominate one named individual to the GPPC Chair (or GPPC Secretariat). In the event that the nominated named individual is unable to participate in a specific meeting or activity of the Working Group, the GPPC member may nominate an alternative named individual.

37. The term of office of any member of a Working Group shall be from one GPPC General Meeting to the next.

38. The names of participating organizations and their representatives in each Working Group will be included in the GPPC web site.

MEANS OF WORKING

39. These Working Groups may operate by means of meetings, workshops, and other events, as well as using electronic and other communication tools.

40. Working Groups may also decide, if they wish, to constitute permanent or temporary task forces or committees to consider and advise on specific issues or individual or groups of targets. These subgroups will report to the Chair of the Group.

COMMUNICATIONS AND REPORTING

41. Communications between the Working Groups and the SCBD will normally be via the GPPC Chair and Secretariat.

42. Working Groups will be expected to provide an update on their work to the GPPC Chair on at least an annual basis.

Reporting

43. No formal reporting requirements will be required of members of the Partnership, except within the context of the activities of the Working Groups. However, participating organizations are encouraged to provide relevant information regularly, particularly relating to existing or planned activities concerning the implementation of the GPPC program of activities, or other policies, activities, and initiatives relevant to GSPC implementation. Such contributions can be included in or linked to the GPPC web site and made available to the Executive Secretary of the CBD, the Parties, and the flexible coordination mechanism for the GSPC to implement the Strategy and help monitor progress in the achievement of the 16 outcome targets by 2020.

SUPPORTING TARGET 4 OF THE GLOBAL STRATEGY FOR PLANT CONSERVATION BY INTEGRATING ECOLOGICAL RESTORATION INTO THE MISSOURI BOTANICAL GARDEN'S CONSERVATION PROGRAM IN MADAGASCAR[1]

Chris Birkinshaw,[2] *Porter P. Lowry II,*[3,4] *Jeannie Raharimampionona,*[2] *and James Aronson*[3,5]

Abstract

The Missouri Botanical Garden (MBG) is supporting community-based conservation at 11 priority areas for plant conservation in Madagascar. Our strategy for conserving these sites integrates a range of activities that include research and monitoring, the creation and policing of local rules to enable the sustainable use of natural resources, environmental education, the provision of alternatives to the unsustainable over-exploitation of natural resources, poverty alleviation, and the restoration of degraded ecosystems. While this approach is successfully conserving biodiversity in the short term and at local scales, over a longer time period these reserves will become increasingly threatened by a rapidly growing human population whose livelihood is dependent on natural resources that will become increasingly rare outside of protected natural areas. Extensive ecological restoration of landscapes surrounding reserves is a prerequisite in Madagascar for the long-term conservation of these protected areas and will thus be an essential part of a national effort to achieve Target 4 of the Global Strategy for Plant Conservation (GSPC). Here, we describe our current restoration program, analyze its strengths and weaknesses, and consider the threats and opportunities relating to restoration in Madagascar. This information is used to identify key attributes for a proposed up-scaled restoration initiative that can serve to develop more sophisticated methods, strengthen expertise through training, and demonstrate the power of ecological restoration for achieving long-term, sustainable conservation outcomes, as called for by the GSPC.

Key words: Ecological restoration, Global Strategy for Plant Conservation (GSPC), Madagascar.

With an area of 587,040 km^2, roughly similar to the area of California and Arizona combined, the island nation of Madagascar has a remarkably diverse flora that comprises nearly 12,000 species of vascular plants already described, belonging to over 900 genera and 239 families (Madagascar Catalogue, 2013a), plus as many as 2000 additional species that remain to be scientifically named (Phillipson et al., 2006). In comparison, the flora of North America includes around 20,000 native species in an area more than 40 times as large. Even more striking is the level of endemism in the Malagasy flora, which was recently estimated as 84% of the published vascular plant species, and an even more remarkable 35% of the genera (Callmander et al., 2011), figures that will increase as new taxa are described. However, this exceptional botanical wealth, which also includes five endemic families, is acutely threatened because of the immense ecological footprint of the rapidly growing, largely very poor, human population

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(2.65% demographic growth per year; Central Intelligence Agency, 2013).

Madagascar's rural people rely on subsistence agriculture for their livelihoods, yet nearly all increases in agriculture come at the expense of natural ecosystems. Between 1950 and 2005, the country lost 40% of its cover of forest, woodland, and thicket (Harper et al., 2007), and during this same period many plant species undoubtedly went extinct. Today, almost all of the island's exceptional flora is threatened by habitat loss, making Madagascar one of the five hottest of the world's 34 recognized biodiversity hotspots (Mittermeier et al., 2004). This situation underscores the urgent need for coordinated action, as called for by the Global Strategy for Plant Conservation (GSPC) as established in Montreal (Convention on Biological Diversity [CBD], 2011a, 2011b, 2011c, 2011d), with its far-reaching set of objectives and targets.

In this paper, we explore how the ecological restoration activities now being developed and conducted by the Missouri Botanical Garden's (MBG) conservation program in Madagascar could be expanded to contribute significantly to the implementation of the GSPC in Madagascar, and in particular to the GSPC Target 4, which calls for securing "at least 15% of each ecological region or vegetation type by 2020 through effective management and/or restoration" (CBD, 2011d).

Missouri Botanical Garden's Conservation Activities in Madagascar: A Platform for Developing Ecological Restoration

MBG supports active programs in more than a dozen countries. The largest of these programs is in Madagascar, where over the last 25 years the organization has developed a program with over 100 local staff members conducting a wide range of activities. Initially, the program focused on botanical exploration, taxonomic research, and in-country capacity building, with a special emphasis on training. Led by our local field botanists, MBG has conducted one of the world's most productive modern field inventory programs, and our staff has made a large contribution to understanding the Malagasy flora. The results of these efforts have been made available to the world through the publication of scores of taxonomic revisions, species descriptions, and the online publication of the Catalogue of the Vascular Plants of Madagascar (Madagascar Catalogue, 2013a). Starting in the late 1990s, local members of MBG's staff in Madagascar came to the realization that plant conservation efforts were far from adequate, which instilled a growing desire to play a more direct and active role in achieving realistic conservation goals.

As an initial step toward addressing the critical need for expanded plant conservation efforts, we used the large body of information on Madagascar's flora gathered over the last quarter century to identify priority areas for plant conservation, the goal of which was to ensure that no plant species are lost to extinction. In 2001, a total of 78 priority areas were identified (Andriambolonera & Raharamampionona, 2005; Raharimampionona et al., 2006). The following year, we launched a pilot project to conserve one of these priority areas, the Agnalazaha Forest, a rare fragment of littoral forest, one of Madagascar's most highly threatened ecosystems (Consiglio et al., 2006). We adopted a community-based approach that emphasized a combination of conservation of native ecosystems, environmental education, and sustainable local economic development. Based on the success achieved at Agnalazaha, we embarked on an expansion of our program over the last decade, and today we are working with local communities at 11 priority sites with a total area of nearly 60,000 ha. These sites are situated throughout the country and encompass a broad diversity of vegetation types, including dry forest and thicket (Anadabolava and Oranjia), littoral forests (Agnalazaha and Pointe à Larrée), low-elevation humid forest (Analavelona, Analalava, Makirovana-Tsihomanaomby, Vohibe, and Ankarabolava-Agnakatrika), sclerophyllous woodland and shrubland (Ibity Massif), and mid-elevation humid forest (Ankafobe). All but one of these 11 sites, the tiny Ankafobe Forest managed as a community reserve, have now been formally accorded temporary protection by the Malagasy government, the first of two stages in the process leading to the forest's permanent designation as an official, nationally recognized protected area.

The approach used by MBG to achieve long-term conservation at each site involves basing a full-time, well-trained, and highly motivated Malagasy Conservation Facilitator within the community, located close to the conservation site. This person engages local stakeholders in a negotiation process that leads to a mutually acceptable delimitation and management zonation for the conservation site, and the Facilitator works with the stakeholders to develop and implement a set of community rules (*dina*) that are grounded in traditional customs and specifically designed to support sustainable management of the area's natural resources. To mitigate the negative impact of restricting access to the natural resources contained in the area being conserved, MBG also works with a local Management Committee, which we

help to set up, to develop alternative resources for community members, and to identify and implement alternative income-generating methods for those persons whose livelihoods are most heavily affected. This basic approach is supported by ongoing research, monitoring, and information-sharing to enable informed decision-making by MBG, the community, and government agencies. In addition, sustainable economic development is actively promoted in these communities in order to reduce poverty and the resulting tendency to rely on the non-sustainable exploitation of natural resources. Examples of sustainable activities prompted at our sites include fish farming, organic gardening, nature tourism, and community-based plant nurseries.

The conservation program at each of the 11 sites where MBG is involved also includes a number of activities that contribute to ecological restoration, which may be defined as the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed Society for Ecological Restoration [SER], 2004). Restoration activities include: (a) the control of particularly harmful, alien invasive plants such as the tea tree (*Melaleuca quinquenervia* (Cav.) S. T. Blake) and guava (*Psidium cattleyanum* Sabine); (b) the reduction of anthropogenic pressures, including burning and the unsustainable harvesting of trees, which constrain natural regeneration and reduce forest cover and integrity; and (c) the reforestation of degraded areas using native species with the aim to restore and expand the remaining forested area. The nature and scale of these actions at each of the 11 sites are summarized in Table 1.

Scaling-up Missouri Botanical Garden's Restoration Activities in Madagascar

While ecological restoration is making a positive contribution to conservation at each of MBG's 11 conservation sites, it is currently doing so within the limited context of a traditional fortress approach to conservation. In most cases, these sites constitute islands that are rich in biological diversity and natural capital but stand isolated in landscapes where these resources are much reduced and where most people are impoverished, relying on marginally productive agriculture for their livelihoods and desperately in need of access to resources. As long as this situation persists, external investment will be necessary to ensure that the natural fortress is not invaded. Although these reserves are successfully conserving biodiversity and providing ecological goods and services in the short term, it seems questionable whether this situation can be sustained over longer periods. A more stable future might, however, be envisaged if the Malagasy economy were to improve significantly and its population were to become less dependent on subsistence agriculture, although this does not currently seem likely. Alternatively, the long-term prospects of these reserves could also be improved significantly if the degraded landscapes surrounding them were to be restored, thus increasing their capacity to satisfy local requirements for natural resources. Thus, in a country such as Madagascar, the extensive use of ecological restoration may well be essential for achieving the sustainable, long-term conservation required to achieve Target 4 of the GSPC (CBD, 2011d).

While MBG's restoration activities in Madagascar are modest, our conservation program has several strengths on which more significant endeavors could be built. These include:

(1) The full-time presence of well-educated and highly motivated staff members at the conservation sites who have won the trust of the local community, have some experience of restoration interventions, and possess an understanding of the site-specific issues that impact whether restoration goals are reached;
(2) Well-developed, multi-faceted community-based conservation programs operating at each site that can facilitate restoration;
(3) A scientific ethos and intimate knowledge of the Malagasy flora that enable a rigorous and efficient science-based approach to restoration;
(4) An integrated network of conservation projects throughout the country that provides an opportunity for developing restoration protocols under diverse environmental and social conditions, and that facilitates the exchange of experience between restoration practitioners; and
(5) The presence at each site of largely intact natural vegetation that can provide both a reference ecosystem for setting restoration goals and key resources such as plant material and top-soil for implementing restoration activities.

The successful expansion of restoration activities at our sites will, however, require overcoming three major weaknesses. First, there is a paucity of public land near some of the 11 reserves that could be used for community-based restoration projects, which will require that we work closely with private landowners whose short-term land-use goals may be difficult to reconcile with the long-term goals of restoration. Second, there is a limited level of expertise and experience among our staff with regard to developing a robust restoration program and carrying out the full range of technical aspects needed for implementing

Table 1. Restoration activities at the 11 priority areas for plant conservation where the Missouri Botanical Garden is now facilitating conservation, restoration, and sustainable local economic development in Madagascar.

Site	Reforestation	Control of invasive alien species	Promotion of regeneration by reducing factors leading to ecosystem degradation
Agnalazaha	• Seedlings of native tree and shrub species propagated in village nurseries and planted in anthropogenic forest clearings (over six years, 30,000 seedlings produced and planted over 9 ha) • Research conducted to inform planting protocols (comparison of growth and mortality of seedlings with and without added compost in their planting holes)	• The local management committee supported for the establishment and implementation of local rules (*dina*) that encourage the use invasive species • *Melaleuca quinquenervia* felled in over 50 ha	• Risk of burning by wild fires reduced by creating firebreaks and by supporting fire-spotting teams during the dry season • New shifting cultivation stopped and exploitation of wood products (timber, fence posts, fuel) controlled by supporting the management committee in the development and application of local rules for forest use
Anadabolava			• New shifting cultivation stopped and exploitation of wood products controlled by supporting management committees in the development and application of local rules for forest use
Analalava	• Seedlings of native tree and shrub species propagated in village nurseries and planted in anthropogenic clearings within the forest (over six years, 31,000 seedlings produced and planted over 10 ha) • Research conducted to inform planting protocols (comparison of growth and mortality of seedlings with and without added compost in their planting holes) • Research conducted to define protocols for the vegetative propagation of native trees	• Research conducted to inform the development of a plan to control *Psidium cattleyanum* (comparison of costs and efficacy of various methods of controlling this invader)	• Risk of burning by wild fires reduced by encircling forest with a firebreak • Exploitation of wood products stopped by supporting a management committee in the development and application of local rules for forest use
Analavelona			• Risk of burning by wild fires reduced by creating firebreaks along the edge of parts of the forest that are most vulnerable to burning
Ankafobe	• Research conducted to inform the development of a restoration plan (classification and mapping of vegetation types and description of vegetation succession following forest felling and burning) • Anthropogenic grassland surrounding forest reforested using locally produced native tree seedlings (since 2005, 21,000 seedlings planted over 8 ha) • Research conducted to inform planting protocols (comparison of growth and mortality of seedlings in different size classes at time of planting) • Research conducted to inform planting protocols (comparison of growth rate of seedlings of four native pioneer species planted in anthropogenic grassland under two conditions: control versus added compost, mulch and shade)		• Risk of burning by wild fires reduced by encircling the forest with a double firebreak and supporting fire-spotting teams

Table 1. Continued.

Site	Reforestation	Control of invasive alien species	Promotion of regeneration by reducing factors leading to ecosystem degradation
Ankarabolava-Agnakatrika	• Research conducted to develop best protocols for the reforestation by the direct sowing of seeds of native trees in the sites where they will grow to maturity • Areas of former cultivation reforested within the forest using locally produced native tree seedlings (over one year, 3500 seedlings planted over 2 ha)		• Exploitation of wood products controlled by supporting several management committees in the development and application of local rules for forest use
Ibity Massif			• Research conducted to inform the development of a restoration plan for the site (relationship between fire frequency and vegetation types)
Makirovana-Tsihomanaomby	• Seedlings of useful native tree species propagated in village nurseries and planted in anthropogenic clearings within the forest (activity began in 2011)		• Exploitation of wood products and use of fire as an agricultural tool controlled by supporting several management committees in the development and application of local rules for forest use
Oranjia	• Seedlings of useful native tree species are propagated in village nurseries and planted in anthropogenic clearings within the forest (over two years, 3000 seedlings produced and planted over 4 ha)	• Research conducted to develop saleable, wooden handicrafts that could be made by local people using invasive alien species as an economic alternative to the exploitation of timber	• Exploitation of wood products controlled by supporting several management committees in the development and application of local rules for forest use
Pointe à Larrée	• Seedlings of native tree and shrub species propagated in village nurseries and planted in anthropogenic clearings within the forest (over three years, 23,000 seedlings produced and planted over 5 ha)	• *Psidium cattleyanum* controlled by uprooting and replanting the area it occupied with seedlings of native species	• Exploitation of wood products and use of fire as an agricultural tool controlled by supporting several management committees in the development and application of local rules for forest use
Vohibe	• Seedlings of native tree and shrub species propagated in village nurseries and young individuals planted in anthropogenic clearings within the forest (over six years, 50,000 seedlings produced and planted over 14 ha)		• New shifting cultivation stopped and exploitation of wood products controlled by supporting a management committee in the development and application of local rules for forest use

such plans. Third, to date, our restoration activities have been limited by funding constraints.

In addition to these strengths and weaknesses, several major external opportunities and threats will have to be taken into consideration as we develop restoration work at our sites. One important opportunity is the desperate need for new sources of income by rural populations in Madagascar, which strongly implies that if restoration projects are designed to maximize employment opportunities then they will likely receive strong support from local stakeholders and could contribute significantly to reducing poverty and the unsustainable use of natural resources. Another key opportunity is the presence in some parts of the country of large areas of degraded land that are currently perceived to have little value and thus could be made available for restoration projects without generating conflict with other land users. A significant threat, however, is presented by Madagascar's widespread poverty and the associated tendency to make land-use decisions that address short-term needs at the expense of compromising long-term options. Another threat is the current paucity of donors whose funding strategy is compatible with supporting the kind of long-term commitment needed for restoration projects to be successful. However, it is possible that the current REDD+ negotiations within the United Nations Framework Convention on Climate Change (UN-REDD Programme, 2009; Alexander et al., 2011), as well as discussions and ongoing projects under the CBD convention and the United Nations Convention to Combat Desertification (UNCCD, 2012), may lead to new funding opportunities for restoration in the coming decade.

The best approach to restoring the degraded ecosystems and fragmented landscapes in which the MBG's 11 conservation sites are situated will be to expand restoration activities to exploit these strengths and opportunities while addressing weaknesses and mitigating threats. These activities should seek to: (1) retain and strengthen local expertise; (2) encompass complimentary elements such as education and economic development; (3) employ a scientific approach that promotes regular evaluation and improvement throughout the life of the project; (4) promote the exchange of ideas and experience among restoration practitioners working at all 11 sites; (5) develop protocols that maximize the sustainable use of the natural resources available at each site; (6) seek incentives for private landowners to support restoration even if this sometimes requires adopting an approach that does not aim to restore entirely natural ecosystems; (7) increase MBG's capacity to design and implement ecological restoration; (8) exploit low-technology restoration methods that maximize rural employment opportunities; (9) focus restoration on highly degraded landscapes that have little current economic value; (10) collaborate with development organizations to reduce poverty in the vicinity of restoration projects; and (11) mobilize the full force of the botanical garden and conservation communities to secure support for expanding restoration projects and programs to ensure that restoration can make a significant contribution to biodiversity conservation and to achieving the targets set by the GSPC (CBD, 2011a, 2011b, 2011c, 2011d; cf. Hardwick et al., 2011).

The Importance of Model Restoration Projects to Inspire and Inform Expanded and More Effective Restoration Endeavors in Madagascar

MBG's current restoration activities in Madagascar are relatively simple and small scale, typical of those being implemented by other conservation organizations operating there and in many other developing countries. Two notable larger-scale restoration projects involving several hundred hectares are being undertaken in Madagascar at Fandriana-Marolambo (Roelens et al., 2010, unpub.) and within the Ankeniheny-Zahamena Corridor (Conservation International, 2011), but even they lack the sophistication of flagship restoration efforts elsewhere in the tropics, such as in Costa Rica (Janzen, 2002) and southeastern Brazil (Rodrigues et al., 2010). For the most part, restoration in Madagascar primarily aims to curtail human activities that lead to forest degradation and, thereby, promote natural regeneration while also planting native trees in areas where natural forest regeneration is thought to be blocked (Holloway, 2007). No projects effectively tap the full potential of large-scale, science-based ecological restoration for contributing to the conservation of Madagascar's biodiversity, increasing the country's natural capital, and promoting resiliency against climate change. Moreover, none of the current restoration projects can be regarded as a model of best practice for achieving effective ecological restoration. While Target 4 of the GSPC (CBD, 2011d) specifically calls for restoration, conservation decision-makers and technicians in Madagascar lack awareness of and exposure to successful restoration efforts, and they remain unconvinced of the importance of restoration. Model projects are, thus, urgently needed to increase the pace of progress toward achieving the GSPC Target 4. This will require additional investment and visibility, which MBG's conservation projects are in an excellent position to facilitate. Thus, while the long-

term conservation of MBG's 11 priority areas for plant conservation will require greater investment in restoration than at present, if this scale-up can be done in such a way as to create a series of model restoration projects, then our contribution to achieving the GSPC Target 4 in particular, and to promoting biodiversity conservation and improving human livelihoods in Madagascar in general, would be significant.

In conclusion, the experience we have gained from conserving 11 priority areas for plant conservation in Madagascar suggests that ecological restoration will be a prerequisite in most situations for successful long-term conservation and, therefore, must be an essential element in a national effort to achieve Target 4 of the GSPC (CBD, 2011d). However, despite the importance of ecological restoration, its current application in Madagascar is both small in scale and technically primitive. To help overcome these issues, MBG is now endeavoring to scale-up the restoration component of the conservation strategies at its 11 conservation sites, some or all of which could be used to test and implement more sophisticated methods, develop expertise through training, and provide operating models to demonstrate the value of ecological restoration for delivering the kinds of lasting conservation and development outcomes called for by the GSPC.

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BUILDING CAPACITY FOR THE ACHIEVEMENT OF THE GLOBAL STRATEGY FOR PLANT CONSERVATION IN THE CARIBBEAN REGION[1]

Colin Clubbe[2]

ABSTRACT

Politically and botanically diverse, the Caribbean region is a biodiversity hotspot. Current estimates for seed plant species richness are nearly 11,000 indigenous taxa, of which approximately 72% are endemic to the region. Politically, the region comprises independent countries as well as overseas territories and countries of the European Union member states and the United States. Success in implementing the 2010 targets of the Global Strategy for Plant Conservation (GSPC) across the region was mixed, and a lack of capacity was consistently cited as a major impediment to full implementation. Several regional initiatives promote coordinated conservation activities and disseminate key information needed for GSPC implementation, including the Caribbean Botanic Gardens for Conservation, whose last meeting in Cuba identified capacity gaps needed for achieving GSPC success. This echoed an earlier regional GSPC workshop held in Montserrat and coordinated by Royal Botanic Gardens Kew and the Secretariat of the Convention on Biological Diversity (SCBD). RBG Kew has an active regional training program and is working with international partners to respond to needs identified locally. This coordinated approach, together with the development of the GSPC Toolkit, can provide a roadmap to meet the challenges of building capacity to achieve the revised 2020 targets in this biodiverse region.

Key words: Botanic gardens, Global Strategy for Plant Conservation (GSPC), networks, training, United Kingdom Overseas Territories (UKOT), West Indies.

The Caribbean region is politically and botanically diverse and comprises an archipelago of more than 1000 islands spread over approximately 3000 km separating the Atlantic Ocean from the Caribbean Sea. Politically, the region comprises 13 independent nations as well as overseas territories and countries of the European Union member states and the United States. A recognized biodiversity hotspot (Myers et al., 2000), current estimates for seed plant species richness are nearly 11,000 indigenous taxa, of which approximately 72% are endemic to the region (Acevedo-Rodriguez & Strong, 2008a, 2008b; Maunder et al., 2008, 2011); however, much of the region is experiencing increasing pressure from the familiar drivers of biodiversity loss, e.g., habitat loss and fragmentation, often driven by development, invasive species, pollution, and, increasingly, the negative impacts of global climate change (Millennium Ecosystem Assessment, 2005; Critical Ecosystem Partnership Fund, 2010).

THE GLOBAL STRATEGY FOR PLANT CONSERVATION

A global analysis of the extinction risk for plants has revealed that more than 20% of the world's plant species are threatened with extinction and that human actions pose the greatest threats to the future of plant diversity (Plants Under Pressure, 2010). The Global Strategy for Plant Conservation (GSPC) aims to halt the current and continuing loss of plant diversity (Convention on Biological Diversity [CBD], 2002) and provides a challenge and opportunity for the international community (Wyse Jackson & Kennedy, 2009). Implementing the GSPC is based on achieving 16 outcome-oriented targets, initially by 2010, and now revised and updated for implementation by 2020 (CBD, 2011a). Achievement of the targets of the GSPC requires considerable capacity, and, consequently, Targets 15 and 16 of the GSPC focus on building capacity. Target 15 focuses on building individual skills and facilities, in particular "The number of trained people working with appropriate facilities sufficient according to national

[1] I would like to acknowledge the many colleagues worldwide who actively support our capacity-building programme and contribute their time and expertise helping us to implement Targets 15 and 16 of the GSPC. I would also like to acknowledge our many alumni who are working so selflessly and making a real difference to the conservation of plants. We have many generous sponsors and funders who make it possible to maintain our capacity-building programme, and with particular reference to activities related to the Caribbean I would like to thank: The Department of Environment, Food and Rural Affairs (Defra), Lennox Boyd Memorial Trust, the Overseas Territories Environment Programme (OTEP), and the Darwin Initiative.

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needs, to achieve the targets of this Strategy" (CBD, 2011d). Although Target 15 focuses on individuals, GSPC Target 16 stresses the collective importance of maintaining networks and partnerships: "Institutions, networks and partnerships for plant conservation established or strengthened at national, regional and international levels..." (CBD, 2011d). The GSPC estimates that the number of trained people working in plant conservation worldwide would have to double by 2010, and although a few national needs assessments have been undertaken, we have fallen well short of this figure (SCBD, 2009). Progress has been made in increasing the number of trained people working in conservation, and several institutions have ambitious international training programs, including the Royal Botanic Gardens Kew (RBG Kew), Chicago Botanic Garden, South African National Biodiversity Institute, and Botanic Gardens Conservation International (BGCI). However, the training impediment remains, and, consequently, Targets 15 and 16 in the revised GSPC 2011–2020 remain almost unaltered (CBD, 2011d). An exciting initiative to help implement the GSPC and to support the attainment of the targets is the development of a web-based GSPC Toolkit, launched in 2011, mediated by the Global Partnership for Plant Conservation (GPPC) and maintained by BGCI (Plants 2020, 2013).

Capacity Building for GSPC Implementation in the Caribbean

The RBG Kew has an active capacity-building program based on courses and individually tailored training on the Kew and Wakehurst Place sites, as well as an active regional program working with in-country partners (Clubbe et al., 2008; RBG Kew, 2011). The International Diploma Programme is the main capacity-building program at Kew and comprises four specialist professional training courses of five to eight weeks in duration. The topics comprise Botanic Garden Management, Plant Conservation Strategies, Herbarium Techniques, and Botanic Garden Education. These courses have recently been reviewed and restructured specifically to support implementation of the GSPC and to provide participants with specific skills and tools in the spirit of meeting GSPC Target 15. The course alumni comprise a powerful network sensu GSPC Target 16 that works on two levels. Such strong bonds are formed within a course that these relationships thrive and form a mutual support network, regardless of where in the world participants return to. Individual course members are then introduced to the wider alumnus via the "On Course" alumnus newsletter; many new relationships have been established via the recognition of common interests or local proximity. To date, 417 participants representing 109 countries and territories have taken a course in this programme, including 30 from 14 Caribbean nations and territories. This forms a powerful international network for implementing the GSPC. Core to this home-based program is the recognition that there is much to be gained from the international flavor and lifelong friendships created by bringing together a group of specialists for a course at Kew. Here, we can draw on wider expertise from, e.g., BGCI, other botanic gardens, and university-based colleagues to provide a stimulating forum for gaining knowledge, sharing experiences, and seeking solutions.

Kew's regional training programme is often based on an existing relationship with a former course alumnus who has returned home after taking one of the Kew courses. While implementing knowledge and skills gained during the Kew course, they identify the need and an opportunity to develop a regional course. In recent years, two such courses have been developed and run in the Caribbean region. In 2007, with funding from the United Kingdom's Department for Environment, Food and Rural Affairs (Defra), Kew teamed up with the Secretariat of the CBD (SCBD) and the BGCI to develop and run a Caribbean regional GSPC workshop. We were collaborating in a Darwin Initiative–funded project in Montserrat at the time (Hamilton et al., 2008) and so worked with our local partners to provide the context and some field experiences to illustrate what implementing the GSPC could look like. The organizing team involved three alumni, including the SCBD's GSPC Programme Officer, and two Montserratian forest officers. The funding enabled us to bring 15 participants from across the Caribbean to Montserrat to discuss GSPC implementation and the barriers to successfully meeting the targets, to review regional activity, and to explore regional cooperation. Experiences varied from Trinidad, where a national GSPC committee was already constituted, to St. Kitts and Nevis, where there was little knowledge at that stage of the GSPC. Significantly, relatively few Caribbean nations had appointed a GSPC national focal point and provided feedback to the SCBD; this has encouraged the implementation of this directive, although there are still only five Caribbean GSPC national focal points (CBD, 2011c). The Plant Conservation Report noted with disappointment that less than one third of parties to the CBD have appointed a national GSPC focal point (SCBD, 2009). The workshop has catalyzed action, e.g., the Trinidad delegate stated that he now had the

framework to provide a re-invigorated agenda for the Trinidad and Tobago national GSPC committee and that this was being implemented. The St. Kitts and Nevis delegate stated that he now had the knowledge to start discussing national implementation.

An active network in the region is the Caribbean Botanic Gardens for Conservation. The network was originally established through a project funded by Cable and Wireless and coordinated by BGCI to strengthen the capacity of botanic gardens in the region for plant conservation and environmental education (Wyse Jackson, 1998). One of the outputs of the project was a conservation action plan, which, although published before the GSPC was adopted, identified many key issues and capacity gaps that still remain unfilled today (Burbidge & Wyse Jackson, 1998). At their most recent conference in Cuba, the network considered progress in implementation of the GSPC as one of its key themes, and presenters reviewed implementation at a global scale (Wyse Jackson, 2010) and a subregional level (Clubbe & Hamilton, 2010), both identifying gaps in capacity and the need to accelerate progress in meeting GSPC Targets 15 and 16 as key issues. Nine alumni from the Kew programme were delegates at this conference, presenting four oral papers and three posters; all are still very active in the field.

A recent review of progress toward implementing the GSPC in the Caribbean revealed that, although success had been variable, substantial progress had been made in many targets in Cuba, Cayman Islands, Guadeloupe, and Martinique in particular (Torres-Santana et al., 2010). The review also identified some of the priority needs and knowledge gaps, including limited financial resources, understaffing, lack of local training and appropriate equipment, lack of adequate protection of important plant areas, ineffective enforcement of environmental laws, limited flow of information, including difficult Internet access, and lack of environmental awareness among the public. Many of these are key needs for capacity building. Torres-Santana et al. (2010) identified the GSPC Target 1, "a widely accessible working list of known plant species, as a step towards a complete world flora" (CBD, 2002), as one of the targets achieved most consistently across the region where it was mostly achieved or good progress noted, with only Anguilla reporting no progress. This is critical because of the underpinning nature of the GSPC Target 1 (Paton & Nic Lughadah, 2011). At a global scale, the launch of the Plant List in December 2010 was a milestone, providing free, easy access to a web-based world checklist of plants (cf. The Plant List, 2013). With any undertaking of this nature and scale, it is a work in progress, and data quality is being regularly improved as a result of feedback and increased knowledge. With the launch of the Plant List, the GSPC Target 1 was achieved and the basis set for achieving the revised Target 1, "an online flora of all known plants," (CBD, 2011d) by 2020. The further implementation of GSPC Target 1 is to provide the same access and information at various scales. At the Caribbean regional scale, the Flora of the West Indies project has brought together a specimen-based distributional checklist for the West Indies that provides access via one web portal to all the indigenous taxa known from this region (Acevedo-Rodriguez & Strong, 2008b). At a subregional scale, the United Kingdom Overseas Territories (UKOT) Online Herbarium project provides a single web-based checklist and botanical information portal (UKOT, 2013). Again, the backbone of this are the plant species lists and specimen information for the five Caribbean UKOTs within the larger database dealing with all 16 territories. This also brings together other botanical resources in support of conservation action on the ground and implementation of the GSPC (Clubbe et al., 2010a). It is vitally important to support in-country partners with training in the core skills needed to use these resources and contribute to their continued use and success. At Kew, specific training is provided in these skills, including plant identification through the Tropical Families identification course as well as providing facilities to use the herbarium and work alongside experienced Kew botanists or taking the Herbarium Techniques course (RBG Kew, 2011). In-country, we work with local partners to put together workshops, courses, or other one-to-one training activities that respond to the identified local needs. For example, in 2007 we ran a Caribbean regional herbarium management course in Trinidad in collaboration with the National Herbarium, which focused on the role of the herbarium in conservation. Twenty-five participants from across the region attended and engaged in lively debate, including opening up herbaria and making their activities more relevant; a GSPC framework helped to facilitate this debate. Access to reliable, up-to-date plant taxonomic information was identified as one of the key barriers, and the development of online databases and online resources such as the digital library of JSTOR (2013) and the Biodiversity Heritage Library (BHL, 2013) are seen as real solutions. The challenge now is to accelerate global access to plant diversity information (Nic Lughadah & Miller, 2009). The production of locally specific field guides is also an important excellent contribution to improving access to plant diversity

information, e.g., the guide to wild plants of Antigua and Barbuda (Pratt et al., 2009).

Targets 1 and 2 of the GSPC go hand in hand. Regional collaboration is vital to achieve GSPC Target 2: "a preliminary assessment of the conservation status of all known plant species, at national, regional and international levels." At a local level, success can be achieved where all the key stakeholders can be brought together in a workshop to assess the species endemic to individual islands and publish a Red List, e.g., the Cayman Islands (Burton, 2008) and Antigua and Barbuda (Pratt et al., 2009). For more widespread species, broader collaboration and data exchange are required, and there now needs to be much greater regional collaboration to achieve the red listing of the whole Caribbean flora. Several initiatives are underway in conjunction with training activities in applying the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories and Criteria (IUCN, 2001); Red List training forms a key component of all the Kew regional courses and workshops. The Plants Under Pressure (2010) report by Kew highlighted that less than 3% of known plant species are currently on the IUCN Red List of Threatened Species, and the GSPC Target 2 activities need to be scaled up significantly if we are to meet the revised Target 2 by 2020. Future progress in plant red listing requires greater participation by the world's herbaria and increased support for expert networks (Schatz, 2009). New tools and techniques, as well as training in their use, are being developed to try and plug this gap (Bachman et al., 2011).

In addition to the sufficiency of trained people noted for GSPC Target 15, Target 16 further emphasizes the need for appropriate facilities, which provides different challenges and resource needs in meeting particular targets; capacity building needs to be directed at targets individually. For example, Kew's Millennium Seed Bank Partnership (MSBP) has an active Caribbean program and supports several local seed collector posts in the smaller islands where resources are very scarce. Training is provided and a collection strategy developed (MSBP, 2013). GSPC Target 8 refers to ex situ collections, at least 75% being preferably in the country of origin (CBD, 2011d). Some of the larger Caribbean countries such as the Dominican Republic are keen to develop their own local seed banking facilities and the MSBP is supporting these developments with technical assistance. However, many of the smaller islands, including the UKOT, prefer to keep their seed in long-term storage off-island and away from electricity surges, power outages, and threats from hurricanes. In these cases, the MSBP is able to offer free storage on mutually agreed terms in the MSBP at Wakehurst Place (MSBP, 2013).

At Kew, seed that is to be banked at the MSBP undergoes germination testing, and key species are grown in the Kew nurseries until flowering; a horticulture protocol is produced, which is shared with country partners. Parallel testing is undertaken in countries where horticultural facilities are available, and training is provided where needed. The protocols enable in-country horticulturists to more successfully grow plants for conservation, restoration, display, and education (Corcoran et al., 2010). It is these types of practical activities that we see as helping build capacity to meet GSPC Target 3: "information, research and associated outputs, and methods necessary to implement the Strategy developed and shared" (CBD, 2011d). These threatened species then go on display at Kew; the stories of these unique plants and their ongoing threats are told to the visiting public. This directly contributes to meeting the GSPC Target 14 on raising public awareness in the United Kingdom. A wide range of awareness-raising activities is also undertaken in the Caribbean as an integral part of all projects. These include talks in schools and to the general public, opportunities for people to join/observe fieldwork, plant naming competitions for endemic species without a local name, and the production of informative posters.

In-country support for developments in botanical infrastructure includes the establishment of native species nurseries with local botanic gardens and national trusts, as well as horticulture skills training where needed (Clubbe et al., 2010b). Native species nurseries provide varied functions. For example, at the Queen Elizabeth II Botanic Park in the Cayman Islands, the use of native species in landscaping is encouraged in response to current usage of non-native, and in some cases, invasive species (Clubbe et al., 2010c). In the Turks and Caicos Islands, the focus is on establishing an ex situ collection of the endemic *Pinus caribaea* Morelet *bahamensis* (Griseb.) W. H. Barrett & Golfari, which is being devastated in the wild by an invasive scale insect. This genetically diverse collection can then form the basis of a reintroduction program once the scale infestation has been controlled.

There needs to be a well-documented way to agree on priorities and actions and to measure success in implementing the GSPC. Consequently, the importance of developing realistic, accurate, and agreed upon management plans is vital. Ideally, species and habitat data should be integrated into an overall habitat-based plan, which links directly to or is

actually part of the National Biodiversity, Strategy and Action Plan (NBSAP) as covered under the CBD (2011b). Achieving the GSPC targets is best integrated directly into this process, and this can be done by facilitating participatory workshops that bring all stakeholders together to agree on requirements and actions and to identify resource needs.

Toward Meeting the GSPC 2020 Targets

Do we have the capacity to achieve the 2020 targets in the Caribbean region? There is good progress in several areas, but many challenges remain. There needs to be greater mainstreaming of the GSPC. We need to increase the number of GSPC focal points to better champion the GSPC locally. Botanical capacity is still a challenge and provides opportunities for the larger, international institutions to work in partnership to help provide focused capacity building. There needs to be a better career structure for botanists and plant conservationists to retain trained personnel. There is still a lack of adequate botanical infrastructure in many places that needs to be urgently addressed. We need to strengthen international partnerships, and we need better support for existing networks to improve what they are already doing. All of these require financial investment at a time when resources are difficult to secure, and plant conservation is not necessarily seen as a priority at a political level. We can work more efficiently by maximizing the use of new technologies and communication tools and can catalyze positive action by exploring the role and use of social networking that is proving to be so successful in many walks of life.

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FROM CHECKLISTS TO AN E-FLORA FOR SOUTHERN AFRICA: PAST EXPERIENCES AND FUTURE PROSPECTS FOR MEETING TARGET 1 OF THE 2020 GLOBAL STRATEGY FOR PLANT CONSERVATION[1]

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Abstract

The exceptional botanical wealth of southern Africa has been known internationally since the early 17th century. However, it is only during the past 25 years that a succession of regional floristic checklists has been published, culminating in one for southern Africa (Namibia, Botswana, Swaziland, Lesotho, and South Africa) (Germishuizen & Meyer, 2003) and another enhanced with primary biological information such as growth form, plant height, and altitudinal range occurrence for South Africa (Germishuizen et al., 2006). These printed products (Germishuizen & Meyer, 2003; Germishuizen et al., 2006) delivered floristic checklists for southern and South Africa, respectively, on time for achieving Target 1 of the 2010 Global Strategy for Plant Conservation (GSPC). These works reflected the cumulative work of several generations of taxonomists, collectors, recorders, and databasers and were based on extensive regional herbarium collections. Two additional goals are now required for the first 2020 GSPC Target, namely adding descriptive and other Flora-style information, and disseminating such information electronically.

Key words: E-taxonomy, Flora of southern Africa (FSA), Global Strategy for Plant Conservation (GSPC), online flora, South Africa, southern Africa.

Consideration of the history of Flora writing for, and in, southern Africa is here undertaken to determine the likely rate of progress with producing an e-flora for the region. One questions whether delivery should or could proceed through conducting an established science in an established way. If a new way of Flora production is to be embraced, for example, through e-taxonomy, then this will inevitably require the overcoming of institutional, social, and technological challenges. Southern Africa is here defined as the Flora of southern Africa (or FSA) region, that is, Namibia, Botswana, Swaziland, Lesotho, and South Africa. We argue that South Africa has been well placed to play a leading role in transforming floristic texts produced prior even to the onset of the world wide web into web-based content that includes nomenclatural and descriptive content as well as plant identification tools.

Brief History of Floras in Southern Africa

Following publication of his *Flora Capensis* in 1823, Carl Peter Thunberg (1743–1828) became widely known as the "Father of Cape Botany." This major work on the Cape flora was preceded by the publication of two volumes of its forerunner, *Prodromus plantarum Capensium*, which Thunberg produced in 1794 and 1800, respectively. Describing just less than 2800 species, Thunberg's *Flora Capensis* was a major reference on the flora of the Cape for the better part of the ensuing 100 years (Gunn & Codd, 1981; Fraser & Fraser, 2011).

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However, this "primary" Flora was antecedent to the *Flora Capensis* initiated by Irish academic William Harvey (University of Dublin) and German apothecary Otto Sonder (Hamburg) (Hall, 1977), which represented the first true Flora for South Africa. It was started privately in the years 1859–1865, within which period the first three volumes were published (Harvey & Sonder, 1859–1860; 1861–1862; 1864–1865). The first significant book on South African botany published on South African soil, *The Genera of South African Plants*, was produced by Harvey about 20 years earlier in 1838 (Bullock, 1978; Gunn & Codd, 1981: 180). This marked the year that the comprehensive exploration of the South African interior gained momentum through a northerly and easterly Great Trek undertaken by the Boers who were, mostly, dissatisfied with British colonial rule following the second and final British invasion in 1806. Sir William Hooker was attributed with "urging its [*Flora Capensis*] prosecution on its originator, Dr. Harvey," although Kew was not at first formally involved in this colonial Flora (Anonymous, 1861: 259). The Flora series lapsed with the death of Harvey in 1866 and Sonder's disengagement from the project, when in 1875, he sold the greater part of his Cape Herbarium (Gunn & Codd, 1981). Sonder died in 1881, by which time the Philosophical Society of South Africa was already prompting a local dignitary to motivate for the completion of the Flora (Hall, 1977). After a lapse of 15 years, the Flora resumed in 1896 under the leadership of the Royal Botanic Gardens Kew, with the major portion of the work completed by N. E. Brown and C. H. Wright of that institute. A number of South African botanists also contributed treatments, however, including H. Bolus, F. Guthrie, E. Stephens, H. Pearson, and E. Phillips (Thiselton-Dyer, 1925; Phillips, 1930). The final fascicle of *Flora Capensis* (Hill, 1933), on gymnosperms, was printed as a supplement to Volume V. In total, 11,731 species were covered in seven volumes for the area chiefly south of the Tropic of Capricorn. At the time, the series was considered by some, such as J. Burtt Davy who was quoted from his correspondence, as "a permanent and sound foundation for a series of Local Floras of South Africa," and upon which he based his manual of plants of the Transvaal and Swaziland (Thiselton-Dyer, 1925: 291).

In February of 1955, just over 20 years after the final treatise in the *Flora Capensis* series appeared in print, the Botanical Survey Advisory Committee in South Africa unanimously supported the concept of producing an FSA to replace *Flora Capensis*, which was by then perceived as outdated. It was anticipated at the outset that the project would take about 40 years to complete, eventually covering 20,530 species in 180 angiosperm families. The Minister of Agriculture approved the project in principle, on the condition that the work be published in both Afrikaans and English and that no additional staff be asked for by the Botanical Research Institute (BRI; Verdoorn, 1958). The project was to cover the territories known today as South Africa, Lesotho, Swaziland, and Namibia (Marais, 1958) with the sequence of completion of volumes or fascicles in line with taxonomic revisionary work already in progress. The region then known as the Bechuanaland Protectorate (today Botswana) was to be covered by the Flora Zambesiaca, a project started in earnest during August 1956 and anticipated to take 20 years to complete (Wild, 1958), but which is still in progress. Wild (1958: 54) observed that the proposed Flora Zambesiaca represented "perhaps a more direct collaboration between an independent African herbarium [SRGH] and the European herbaria than in other [Tropical African] Floras which are more definitely the products of European centres." He also pointed out that the boldness of plans for a Flora that would cover what is today Zimbabwe, Botswana, Zambia, Malawi, and Mozambique prompted the South Africans to broaden their floristic vision. Wild (1958) reported that R. A. Dyer, then Director of Botanical Services for the Department of Agriculture in Pretoria, had planned for some years to complete the *Manual of the Flowering Plants and Ferns of the Transvaal with Swaziland, South Africa*, two fascicles of which had been produced by Burtt Davy (1926, 1932). However, learning of the scope of the Flora Zambesiaca project, Dyer decided rather to co-motivate for a much more ambitious FSA. This Flora was to complement the Flora Zambesiaca and the *Conspectus Florae Angolensis* and with them provide a complete floristic review of the whole area south of the Congo and Tanzania (Dyer, 1977).

The first FSA volume was generally well received on its publication in 1963, with a reviewer (Bullock, 1965: 224) observing that "throughout the text there is most encouraging evidence of the effectiveness of the Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale (AETFAT), the main objects of which are to encourage international discussion of taxonomic problems and to attain a high degree of uniformity in both taxonomic treatment and nomenclature in all the regional Floras currently in preparation." Dyer (1977) similarly acknowledged the role of AETFAT, which first convened in Brussels in 1951, in providing impetus to the preparation of regional Floras. Not surprisingly, AETFAT meetings

have provided a regular opportunity for taxonomists to present on progress with the African Floras (e.g., Codd, 1965, 1968; Killick, 1971, 1976 for the FSA). Although AETFAT has continued to meet every three or four years over the past six decades, Flora reports have appeared less regularly in the proceedings resulting from recent conferences (sometimes presented only as posters), most notably for those Flora series that have progressed rather slowly.

Other than the FSA series undertaken by the then BRI of South Africa, often with overseas international collaborators, workers within several of the countries included in the geographical scope of the FSA contributed significantly toward Flora studies for their respective nations. Compton (1976) delivered *The Flora of Swaziland*, which treated 2118 species of flowering plants, providing brief descriptions as well as taxonomic keys, collection vouchers, and notes on ecological and taxonomic matters. A subsequent updated checklist (Braun et al., 2004) enumerates 3441 plant taxa from Swaziland, reflecting substantial botanical exploration of that country during the past four decades; Compton's Flora nonetheless remains a useful basis for delivery on Swaziland's Target 1 for GSPC by 2020. The Flora of South West Africa (FSWA), of the country known today as Namibia, was previously treated as a prodromus, a preliminary treatise respecting a subsequent more elaborate work as was intended by Merxmüller (1968). His part 1 (of five, by 1972) first appeared in 1966, some 15 years after the work initiated, it was anticipated that it would be possible to complete the entire work within three years thereafter (Merxmüller, 1968). Ultimately, publication would proceed over six years (Merxmüller, 1966–1972) and represent the treatment of ca. 4300 taxa from an area of 824,268 km^2. The early completion of Merxmüller's prodromus has well placed the taxonomic community in Namibia to further research and manage its flora, a good reminder that even the completion of a flora's prodromus, as would be the case with a Flora, is a means to further ends and not just an end in itself. Among the 10 participants in the Southern African Botanical Diversity Network (SABONET) program, Namibia has been outstanding in its delivery of useful products. It was the first to produce a country plant checklist (Craven, 1999) and a country-level plant Red Data Book (Loots, 2005). Presently, a modern, English-language Flora of Namibia is under development.

By the late 1970s it was realized that in order for the volumes to appear in the form planned initially, the progress with the FSA would need to proceed much more rapidly (see Dyer et al., 1963: vi–vii). Accordingly, the format of the Flora was modified (descriptions were shortened and specimen citations simplified) to speed up production without the loss of essential information, and fascicles with a minimum of 50 species were considered for publication (Leistner, 1983). This necessary change reflected a flaw in the original Flora planning process, which led to components of volumes being completed but not printed, as the balance of the anticipated contents was not ready for publication. As part of efforts to enhance the publication rate of small, but publishable units submitted to the FSA editorial office, the series "FSA contributions" within *Bothalia* was started in the mid-1990s (see, e.g., Smith, 1995a, 1995b). As conceived, the Flora was to appear in 33 volumes with some volumes split into a maximum of four parts for very large families, for example, Asteraceae, such that between 300 and 800 taxa would be treated per volume. Although information for inclusion in the planned FSA was considered by Verdoorn (1958: 74) to be "on the generous side," standard Flora-style information was ultimately presented. Each taxon and its relationships in both southern Africa and adjoining territories were considered critically, and taxonomic descriptions, keys, selected citations of specimens and literature given, along with distributional information, synonyms, nomenclatural types, notes, and at times illustrations.

At the present time, ca. 18% of the 24,393 plant taxa known from southern Africa (Germishuizen et al., 2006) have been treated in the FSA, and this after 55 years of work. The vast majority of treatments deal with South African species, which were recently enumerated at 22,604 taxa (Germishuizen et al., 2006). By 1970 alarm bells were already ringing, and Killick (1971: 77) reported to AETFAT that at the rate of progress then evident, although parallel monographic work was not included in the FSA, "the Flora will take another two centuries to complete." Five years later Killick (1976: 633) balefully projected that the Flora would be completed in 2345, although if one included the species already completed in the volumes then being tackled "the situation looks a trifle brighter: 8% completed and final date 2151." De Winter (1970) had estimated that five fully trained taxonomists dealing with 150 species per year would take only 18 years to complete the FSA. However, Killick (1971: 77) pointed out that although seven professional botanists were working on the Flora team, none worked full time on the project, resulting in "a most unsatisfactory state of affairs." Leistner (1983) appealed to members of AETFAT to cooperate on the FSA, noting that 48

taxonomists from outside the BRI of South Africa were already collaborating. However, it is likely that the apartheid policies of the then government of South Africa deterred participation, and within a few years an academic, cultural, and sports boycott of the country was in full motion. At the time, the other major African floras (Flora Zambesiaca, Flora of Tropical East Africa) were also struggling to improve their slow production pace, and most European taxonomists were already committed to those projects.

Collaboration North-South and South-South

Most large Flora projects, both historical as well as current, are clearly undertaken by major international herbaria such as those of the Royal Botanic Gardens, Kew (K) and the Missouri Botanical Garden (MO). Indeed, significant taxonomic achievements that yield regional Floras or checklists in sub-Saharan Africa have most often resulted from collaborations between north and south. The FSA is exceptional in that it has been attempted by a developing nation (South Africa), albeit to date with only partial success.

The hugely successful SABONET program, funded by the Global Environment Facility (GEF) and the United States Agency for International Development (USAID), developed through the United Nations Development Program (UNDP), but implemented through the then National Botanical Institute (NBI) of South Africa, represented an almost exclusively south-south collaboration where the main aim was capacity building, but the results included national plant checklists. In the first decade of the 21st century, the nature of such formal collaborations has taken the form of online e-taxonomy, where maximal use of the internet has provided access to regional inventories. In southern Africa, the most recent of these has been the production of inventories of plant diversity and common names for Angola (Figueiredo & Smith, 2008, 2012). The plant diversity inventory was supplemented by a wealth of biodiversity data available electronically and through the international collaboration of 30 scientists (Smith & Figueiredo, 2010). Online resources accessed in the course of this floristic work are detailed by these authors.

One of the most significant north-south projects for Africa to have been completed in recent years is the first-ever angiosperm checklist and database for sub-Saharan Africa (Klopper et al., 2006). The African Plant Checklist and Database project (APCD) is a collaboration between the South African National Biodiversity Institute (SANBI) and the Conservatoire et Jardin Botaniques de la Ville de Genève (Switzerland) and is available as a regularly updated online searchable database (African Plant Database, 2013). In line with the objectives of AETFAT, the APCD checklist was conceived in 1994 during the 14th congress of that Association; the full history of the project has been documented by Gautier et al. (2006).

Global Strategy for Plant Conservation Target 1 for 2020

The original Target 1 of the Global Strategy for Plant Conservation (GSPC; United Nations Environment Programme [UNEP], 2002) was conceived as "a widely accessible working list of all known plant species, as a step towards a complete world Flora." This target was considered well addressed when a global world plant list became available (Plant List, 2010) in late December 2010. In southern Africa, such a target had been achieved years earlier with the national checklists produced within the scope of the SABONET program (Craven, 1999; Braun et al., 2004; Kobisi, 2005; Setshogo, 2005; Germishuizen et al., 2006) and by the global sub-Saharan checklist for flowering plants (Klopper et al., 2006). Further progress toward delivery on this target for several components of the South African flora prior to 2010 has been provided by Smith and Smith (2006).

Looking ahead to the next stated interval, 2011–2020, the Global Partnership for Plant Conservation (GPPC, 2010) focuses on the enhancement of Target 1 with the following goals in mind: a) to add a more complete description and other Flora-style information to the checklist; and b) to make the working list "more useful, accessible, and functional for end-users" by disseminating such information electronically. Therefore, the first target of the GSPC aims now to produce an electronic Flora for all the world's plants by 2020. Significantly, the Secretariat of the Convention on Biological Diversity (SCBD, 1992 on) has unambiguously taken a dim view of the generally slow progress with Flora production globally, by challenging the taxonomic fraternity to produce an electronically accessible Flora for the world within the next seven years.

A recent assessment of the state of botanical research in South Africa (Bredenkamp & Smith, 2008) has highlighted local concerns related to the advancing group age of practicing botanists coupled with an inadequate rate of training and mentoring of young scientists. This gap in age and training is reportedly particularly acute in the formal South African systematics and taxonomic community (Herbert et al., 2001). Nonetheless, as Joppa et al. (2011) have pointed out in their global analysis of rates of species descriptions, systematics research continues

apace, despite such contrary reports on the dissolution of taxonomic capacity. Joppe et al. (2011: 551) determined that "the numbers of [flowering plant] taxonomists are increasing. . .as are the numbers of taxonomists who are the senior authors on species descriptions." This led to their conclusion that "taxonomic description no longer belongs to those who do nothing else; species description is much more widely practiced." However, it must be noted that there is a great difference between describing one new species and producing a taxonomic revision for a group of species, the former being a task eagerly done by amateurs while the latter requires greater perspective and formal training. Regardless of who undertakes the taxonomic work, a strategy and supporting implementation plan for South Africa and southern Africa is required, if Target 1 of the revised GSPC is to be achieved by 2020.

The Way Forward in Southern Africa

The sound nomenclatural and taxonomic platform provided by the APCD supports not only ongoing floristic work in sub-Saharan Africa, but also the e-taxonomic and e-Flora efforts that will be needed by the constituent/participating African countries to support delivery on Target 1 of the 2020 GSPC. This target toward the completion of an accessible or online Flora of all known plants in the world has to build on the achievement of the 2010 target, namely, the working list of known plant species (<https://my-plant.org/news/plant-list-working-list-all-plant-species>). The structure and form of this online Flora are as yet uncertain, even in relation to the scope of content. The current authors consider that it should largely align with traditional concepts of a Flora (see e.g., Harvey & Sonder, 1859–1860) by including descriptive information and identification tools. The traditional format, at least in Africa, has been fairly uniformly modeled and typically concurs with Kirkup et al. (2005: 457), who consider a Flora to "provide an inventory of plants occurring in a particular geographic region and provide a means to identify these plants." Descriptive content and identification tools, such as dichotomous keys, are central to this definition.

Historical, colonial Floras drew on a concise format and taxonomic structure, were mindful of production costs, and provided the minimum needed to allow for the identification of a specimen drawn from, importantly, the defined geographic range for that Flora. With floristic texts and visual resources logarithmically expanding online (cf. Encyclopedia of Life [EOL], now including over a million species pages [Encyclopedia of Life, 2013]), one questions whether the traditional Flora format needs to be maintained, for the historic objectives can now be realized in a completely different way, through a product that might well look and feel vastly different. Importantly though, if a new way of writing and constructing a Flora is to be embraced and Target 1 of the 2020 GSPC achieved, taxonomists and their institutions will need to shift their mindsets, technology base, and approaches to collaboration within an e-taxonomy frame. Significant projects are already underway to harness the interest, expertise, and goodwill of large groups of taxonomists around the globe. The eMonocot initiative (eMonocot, 2013) is one such project that, through the web, will provide information such as up-to-date checklists, nomenclature, taxonomic descriptions, plant images, and identification guides, as well as geographical, ecological, DNA sequence, and conservation data. This is all structured around a taxonomy derived from the online World List of Monocotyledons (2012), which comprise an estimated 20% of flowering plants. If successful in capturing the anticipated data for 70,000 monocot species by 2020, an online world Flora is arguably expanded toward about one fifth of the global GSPC Target 1.

A project to digitize published African Floras was initiated at Kew 10 years ago, with the aim being to improve the accessibility and utilitarian value of the included plant species information (Kirkup et al., 2005). Similar projects have been developed elsewhere, such as the eFloras project hosted by the Missouri Botanical Garden and the Harvard University Herbaria (Brach & Song, 2006; eFloras, 2013). This website includes checklists and Floras for flowering plants and mosses from China, Nepal, Chile, Ecuador, Missouri, and North America, simply the diverse floristics products of active institutional programs. Most of the early e-Floras such as these facilitate access to information published in particular Flora volumes where access is by a quick search by scientific name, sometimes also by synonym, geographical area, or habitat. As indicated by Kirkup et al. (2005), reflecting changes or additions to the published text for the online version of Flora Zambesiaca were out of the scope of these projects. Interrogating these e-Floras will be the same as consulting printed versions of the Floras in a library, but quicker and more globally accessible. Links to other databases for updated nomenclature are sometimes provided, but such searches may yield irrelevant or inadequate information for the taxon being searched. More recently, other e-Floras have been established, such as the Flora of New Zealand (Flora of New Zealand Committee, 2013), where

information from the original published Flora is dynamically supplemented with data from other sources and with links to other websites. In the near future, it is expected that e-Floras will evolve further, with direct links to information associated with each accepted plant name, and synonymy becoming standard practice. The integration of images of living plants and herbarium specimens (including types) and protologues in an e-Flora is now dramatically achievable. Furthermore, published information from related fields, such as ecology and ethnobotany, where names that are no longer accepted may be used, can also be linked and displayed. This would eventually transcend the function of e-Floras from plant identification tools to plant information systems (enter the ambitious EOL project). This can only be achieved through a collaborative consensus, integrating data from a vast array of different e-sources and with the allocation of resources especially to the most biodiverse areas (Paton, 2009).

The question is then one of how countries such as South Africa should approach Target 1 in order to be able to report at a national level on acceptable country- or regional-level progress toward this target of the GSPC. Whether a taxon-level approach, a geographic approach, or both, is adopted will depend on unfettered access to international initiatives such as eMonocot and its associated e-tools (e.g., the scratchpads so effectively utilized in eMonocots), and on continued, even accelerated progress with traditional Floras or in some instances (e.g., Namibia), development of Floras from their associated prodromi.

During the next eight years South Africa will adopt a dual-pronged approach in evolving e-taxonomy opportunities and existing commitments to provincial and biome-focused Floras, a number of which have already been completed. As early as the 1970s it was realized that the slow progress of the tradition-based FSA would take centuries to complete, and through the efforts of Bond and Goldblatt (1984), the first Flora-style treatment of the Cape Floristic region was published. This work has since seen a second comprehensive update (Goldblatt & Manning, 2000), with a third version now in print production. Similar but with a slightly different style and content, Retief and Herman (1997) produced a taxonomic treatment of the plants of the northern provinces of South Africa. Although the two regions, separated by South Africa's arid, karroid interior, have some species in common, the intelligent digitization of both tomes would provide a significant e-backbone for about 10,000 South African plant taxa. In addition, Retief and Meyer (in prep.) have made significant progress with Plants of the Free State, Snijman (in prep.) with the greater Cape Flora, including the succulent karoo biome, Bredenkamp (in prep.) with the Eastern Cape Flora, and the Northern Cape Flora (Magee & Boatwright, in prep.) having been initiated. This leaves only South Africa's eastern seaboard, essentially from the Drakensberg eastward to the KwaZulu-Natal coast, as lacking treatment. This should offer few challenges, though, as treatments of many species of that subtropical province can be derived from the treatments of the bordering Eastern Cape, Free State, and northern Provinces. These treatments will require significant work to harmonize them across the various in-country regions and to include traditional Flora content that has been occasionally omitted, ranging from protologue and type information, nomenclatural synonymy, as well as adequate identification keys and plant descriptions. It is arguably easier to equalize the treatments than to generate them afresh. The task has been made easier by the availability of much of the necessary information online. It is envisaged that a national e-Flora for South Africa will build from these in-country Floras and various internet resources. These range from taxonomic databases, such as the APCD, JSTOR Global Plants (2013), Kew's World Checklist of Plant Families, the International Plant Names Index (IPNI), and TROPICOS, and also extend to general plant websites such as Plants of Southern Africa (POSA; 2009). An electronic platform can then link all existing information, with additions of original content such as identification tools and distribution maps.

The other southern African countries have much lower plant diversity than that of South Africa (viz. Botswana: 2151 species, Namibia: 3961, Lesotho: 1591, and Swaziland: 3400; Golding, 2002). Electronic Floras for Botswana and Namibia are likely to be produced as outputs of current Flora projects (Flora Zambesiaca and Flora of Namibia) if these reach their end before the 2020 deadline. For Lesotho and Swaziland, e-Floras can be relatively easily accomplished in collaboration and through linking to the resources of the South African e-Flora. Successful delivery of e-Floras in southern Africa will not only require in-country, regional, and international coordination and collaboration with relevant planning, but should also anticipate that developments in information and communication technology (ITC) over the next eight years will provide as-yet unforeseen advantages and tools to develop online Floras.

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ACHIEVING TARGET 8 OF THE GLOBAL STRATEGY FOR PLANT CONSERVATION: LESSONS LEARNED FROM THE NORTH AMERICAN COLLECTIONS ASSESSMENT[1]

Abby Hird[2] *and Andrea T. Kramer*[3]

ABSTRACT

How much progress has North America made toward the Global Strategy for Plant Conservation (GSPC) Target 8 of at least 75% of threatened plant species in accessible ex situ collections by 2020? To answer this, the North American Collections Assessment was carried out in 2010. More than 200 botanical and conservation institutions in the United States, Canada, and Mexico contributed taxa lists to the Botanic Gardens Conservation International's (BGCI) online PlantSearch database for this assessment. By cross-referencing collection information with globally threatened species lists from the International Union for Conservation of Nature and Natural Resources (IUCN), NatureServe, and Mexico's Red List, we found that approximately 35% of North America's nearly 5000 most threatened taxa are currently in ex situ collections. This marks considerable progress toward the GSPC Target 8, but there is clearly much more to do. Future priorities include collaboratively and strategically increasing threatened species representation in collections and assessing genetic diversity among collections by comparing accession-level data.

Key words: Botanic garden, ex situ plant conservation, Global Strategy for Plant Conservation (GSPC), living plant collection, seed bank.

Well-documented, genetically diverse living plant and seed bank collections at botanic gardens and similar institutions support integrated plant conservation (Fig. 1) and provide critical insurance for many of the plant species now threatened with extinction, recently estimated at 100,000 total worldwide (Pitman & Jorgensen, 2002; Guerrant et al., 2004). But how many threatened species are safeguarded in collections, and which are not? While the botanical community as a whole does not know the actual representation in collections of threatened species, the Botanic Gardens Conservation International (BGCI) has a growing number of tools in place to help botanic gardens leverage their collective resources to address this and other challenges ahead.

OUR CONTRIBUTIONS TO THE GLOBAL STRATEGY FOR PLANT CONSERVATION

Botanic gardens have a global mandate to provide a safety net against extinction for threatened plants. The Global Strategy for Plant Conservation (GSPC), ratified by nearly every country in the world, was adopted by the Parties to the Convention on Biological Diversity in 2002 (CBD, 2002). The development and adoption of the GSPC were largely due to the efforts of the global botanic garden community, and we now play a key role in achieving its 16 outcome-oriented targets to halt the loss of plant diversity worldwide. Directly relevant to botanic gardens and their collections, GSPC Target 8 sets a goal to have at least 75% of threatened plants in accessible ex situ collections by 2020. While resources to meet this important target might be limited, the individual and collaborative work of botanic gardens and conservation organizations has made great progress in building ex situ conservation collections as a global safety net for threatened species. As the 2020 deadline approaches, it is critical that we know where we stand relative to this

[1] The North American Collections Assessment was carried out by the Botanic Gardens Conservation International (BGCI) U.S. in partnership with the United States Botanic Garden and the Arnold Arboretum of Harvard University, with additional funding from the Wallace Genetic Foundation. Collaboration with many organizations and botanic gardens throughout North America made this project possible, including the American Public Gardens Association, Center for Plant Conservation (CPC), Canadian Botanical Conservation Network, and Mexican Association of Botanical Gardens. Thanks are extended to all contributors for their support and participation, Suzanne Sharrock and Meirion Jones at BGCI, and special thanks to assessment co-authors Ray Mims, Michael Dosmann, and Kirsty Shaw.

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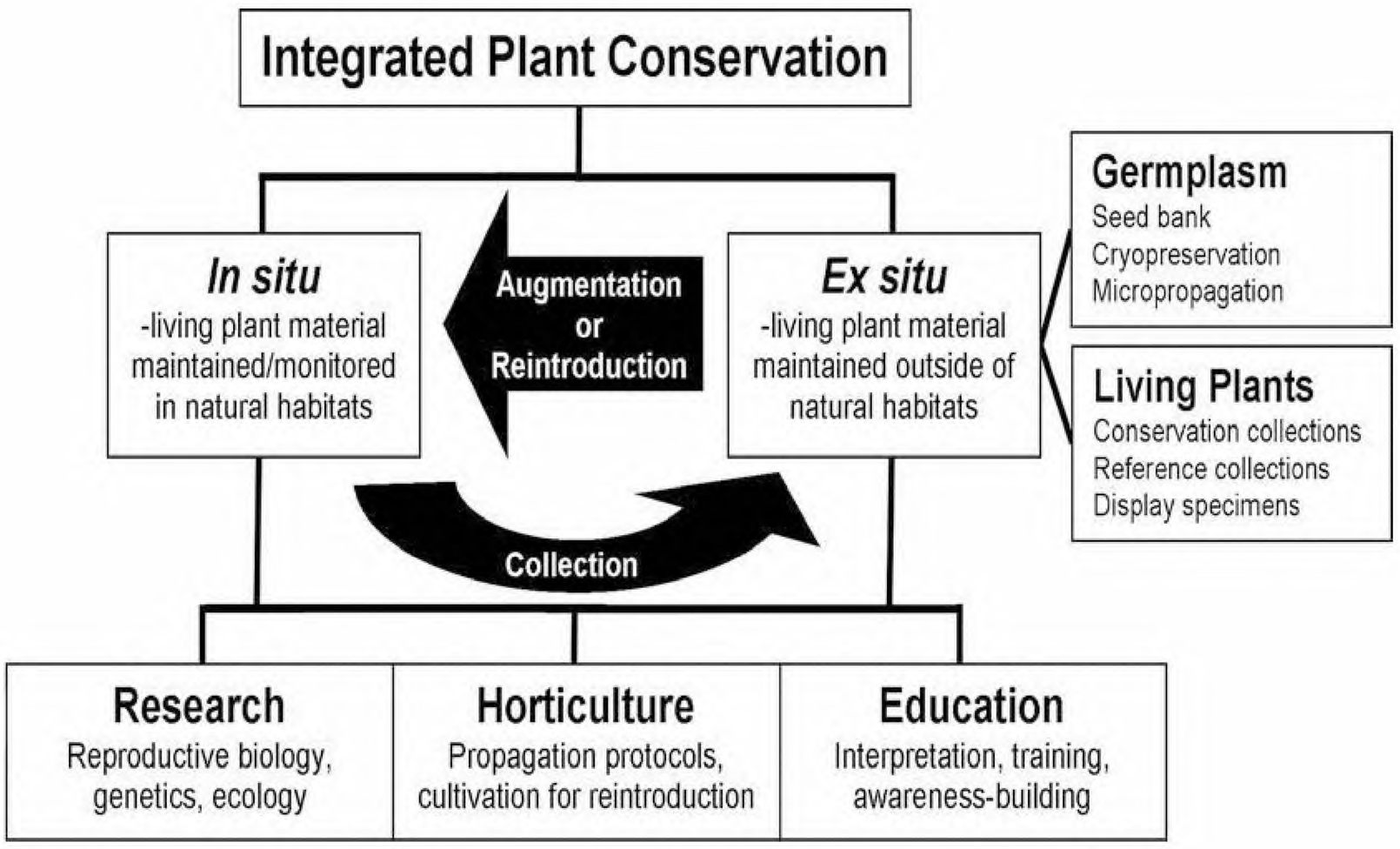


Figure 1. Integrated plant conservation combines in situ (on-site) and ex situ (off-site) conservation action to support species survival. In situ conservation protects species in their native habitat, while ex situ conservation ensures plant material is available for research, horticulture, and education activities that ultimately support reintroduction efforts, ensuring that ideally no species goes extinct.

ambitious target in order to inform future strategic and collaborative conservation efforts.

Measuring Global Progress

When the GSPC was adopted in 2002, the BGCI launched PlantSearch, an online database of botanic garden collections, as a means to measure basic, taxon-level progress toward the GSPC Target 8 (BGCI, 2012b). The PlantSearch database remains the only resource available to measure global progress toward the GSPC Target 8 and represents the only global database of plants in cultivation. All institutions that curate collections of living plants, banked seeds, or other plant germplasm are encouraged to upload a list of taxa in their collections to PlantSearch on an annual basis. This free database not only facilitates estimates of national and global progress toward Target 8, but also provides invaluable data for institutions to prioritize their collection efforts and to connect their collections to other collection holders and researchers nationally and worldwide. This connectivity makes such institutional collaboration and biological research on the conservation of threatened plant species more efficient and effective.

In 2010, the BGCI analyzed the data in PlantSearch and found that only 23% of all threatened plants, i.e., as included on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (IUCN, 2010), are known to be maintained in ex situ collections worldwide. These results are presented in a recent report on botanic gardens and the implementation of GSPC Target 8 (Sharrock et al., 2010). A similar report focused on threatened European plants found that 44% were held in ex situ collections (Sharrock & Jones, 2011). While this indicates positive progress, these results are also a call to action as they fall well short of the 2020 GSPC target of 75%. Highlighted below, the assessment of threatened North American plant species in collections (Kramer et al., 2011) exemplifies both the achievements made and limitations faced in North America as we work to conserve plant species and achieve the GSPC Target 8 by 2020.

Measuring North American Progress

In 2010, the BGCI U.S. partnered with the United States Botanic Garden and the Arnold Arboretum of Harvard University to conduct a North American Collections Assessment, the results of which were recently published and distributed as a report, available online and in print (Kramer et al., 2011). This assessment measured progress toward the GSPC Target 8, specifically within the North American botanical and conservation communities. This project resulted in the first compilation of North American threatened species lists from the varying systems used in the United States, Canada, and Mexico, i.e., NatureServe global threat ranks (NatureServe, 2012), IUCN Red List ranks (IUCN, 2010), and Mexico's NOM Red List (NORMA, 2001; Fig. 2). Taxonomic lists were utilized from over 200 institutions via the PlantSearch database to identify the number of

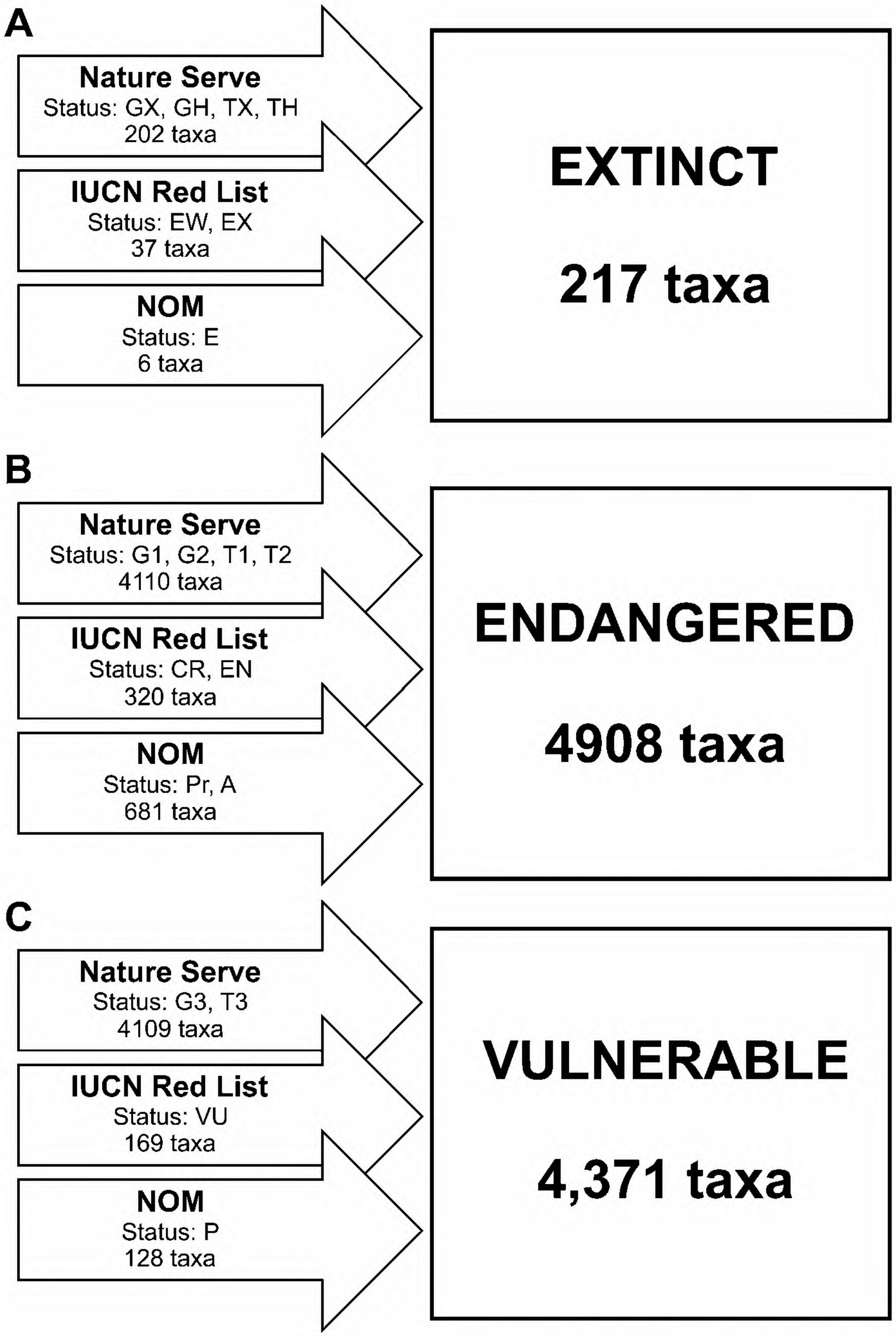


Figure 2. Three threatened species lists (NatureServe for Canada and the United States, NatureServe, 2012; IUCN Red List for plant taxa globally, IUCN, 2010; and the NOM Red List for Mexico, NORMA, 2001) were compiled into three categories (Kramer et al., 2011). —A. Extinct species are represented by NatureServe's assessments of GX or GH (presumed extinct or eliminated or possibly extinct or eliminated) and TX or TH (equivalent to GX or GH, but for a subspecies or variety); by IUCN's EX or EW (extinct or extinct in the wild); and by NOM's E (Probablemente extinta en el medio Silvestre, Probably extinct in the wild). —B. Endangered plant taxa are assessed by NatureServe as G1 or G2 (globally critically imperiled or imperiled) and T1 or T2 (equivalent to G1 or G2, but for a subspecies or variety); by IUCN as CR or EN (Critically Endangered or Endangered); and by NOM as Pr (Sujetas a protección especial, Subject to special protection). —C. Vulnerable taxa are categorized by NatureServe as G3 (globally vulnerable) and T3 (equivalent to G3, but for a subspecies or variety); by IUCN as VU (Vulnerable); and by NOM as P (En peligro de extinción, At risk of extinction). NatureServe rankings may be found at <http://www.natureserve.org/explorer/ranking.htm>; IUCN categories and criteria at <http://www.iucnredlist.org/documents/redlist_cats_crit_en.pdf>; and NOM criteria at <http://www.biodiversidad.gob.mx/pdf/NOM-059-ECOL-2001.pdf>.

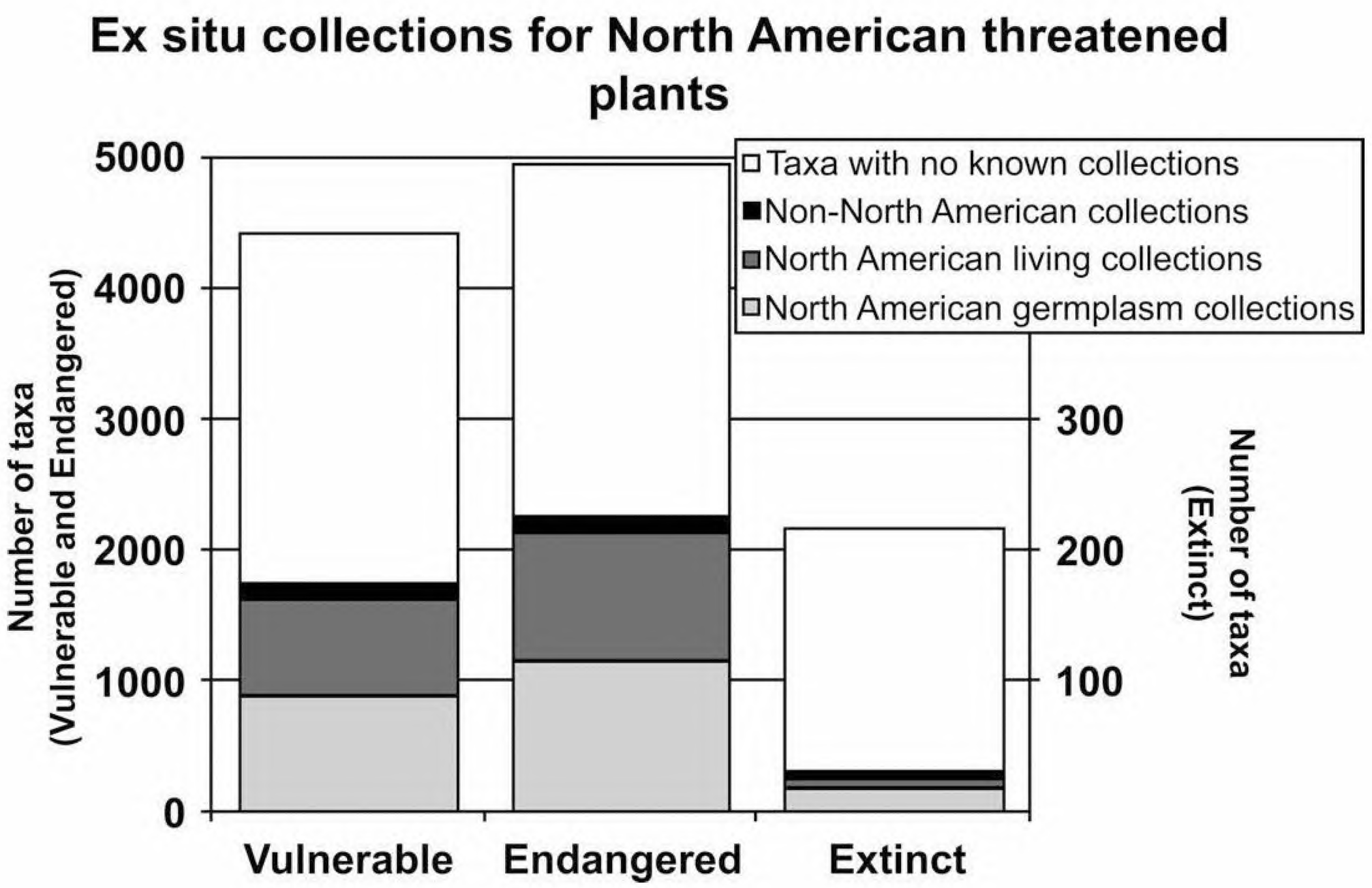


Figure 3. North American threatened taxa in ex situ collections. Threat category corresponds to the summed assessments seen in Figure 2 (endangered, vulnerable, and extinct). Light gray shading refers to germplasm (as seed banked, cryopreserved, or micropropagated material) and dark gray shading refers to living collections (plants). Note the 10-fold difference in y-axes for endangered and vulnerable plant taxa (at left) as compared to the known extinctions (at right).

threatened species maintained ex situ in North America.

Overall, data analyses revealed that 35% of the nearly 5000 most threatened North American species are maintained ex situ either as living plants or germplasm maintained in seed banks or as cryopreserved or micropropagated material (Fig. 3). Of particular concern, we found that nearly half of all endangered plant taxa identified in collections are maintained at only one institution (Fig. 4), which could lead to an ex situ bottleneck and reduction in genetic diversity. Taxa found in only one living plant collection likely exist as one or few specimens potentially of unknown or cultivated origins, which would capture little genetic diversity. This paucity in taxonomically representative specimens might rarely, if ever, be able to support successful reintroductions of extirpated populations.

Conversely, our assessment results are probably a slight underestimate of the number of threatened species in ex situ collections, as only 30% (230) of the known public gardens and similar institutions with living plant and germplasm collections in North America participated in the assessment (http://www.bgci.org/files/UnitedStates/NACA/naca_appendix_1.pdf; Kramer et al., 2011). Efforts were made, however, to ensure that institutions that support conservation of threatened species were able to upload a taxa list to PlantSearch. A large majority of gardens active in the Center for Plant Conservation (CPC) network (90.6%; CPC, 2012) and members of BGCI (85.6%) contributed taxa lists. Further, all but one (54) U.S. gardens reporting an ex situ conservation program in the GardenSearch database were able to contribute to the assessment (BGCI, 2012a). Many of the institutions unable to participate reported insufficient staff or technological resources to provide an electronic list of taxa in their collections. Regardless, these results indicate that we have much work ahead to ensure 75% of North America's threatened species are in accessible ex situ collections by 2020.

Summary and Future Work

It is clear that in order to achieve the GSPC Target 8 by 2020, North American botanical and conservation organizations must increase the number of species held in ex situ collections designed for conservation. Use of information compiled through this and similar assessments can facilitate the prioritization of species acquisitions at individual gardens and aid the broader botanical and conserva-

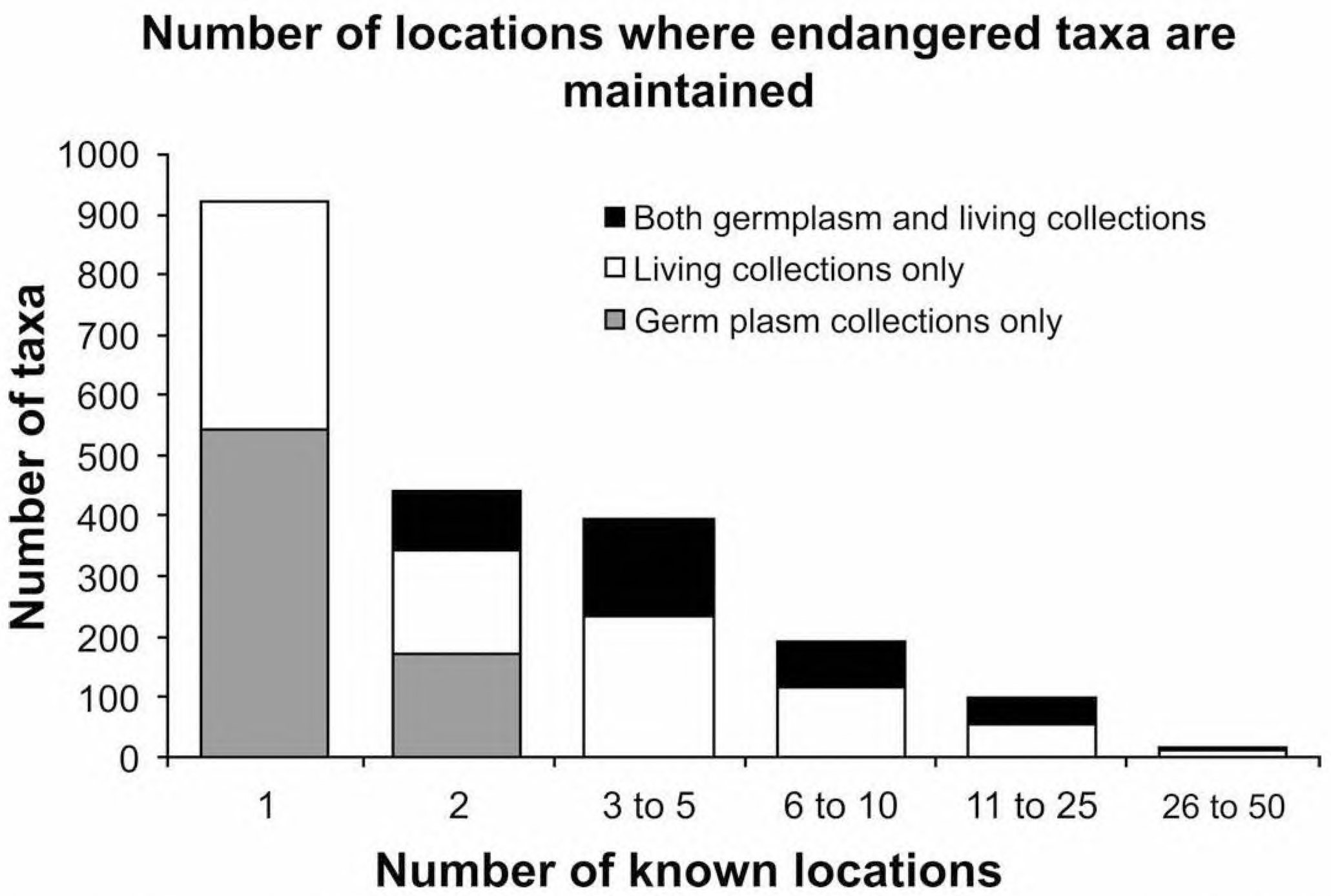


Figure 4. Representation of 2208 North American endangered taxa held in 230 ex situ collections (see Fig. 2 for details). Institutional locations are partitioned by collection type as germplasm (seed banked, cryopreserved, or micropropagated), living plants, or both. Note that many endangered taxa are held at only a single institution.

tion communities to work more effectively toward the successful achievement of Target 8. Additionally, assessments such as this allow progress over time to be documented and monitored, while providing quantitative data that demonstrate the collective impact and value of collections work.

Most institutions with ex situ collections of threatened plants can utilize the integrated plant conservation model to support important conservation, education, and research applications for those species (Fig. 1). Living plant collections in particular can promote threatened species conservation even if they were not designed to have direct, in situ conservation applications. Botanic gardens of every size and scope are uniquely positioned to wield their ex situ collections as tools to educate the public about conservation issues and the importance of plant diversity.

Living plant collection can also be used for research of understudied species (e.g., life history, ecology, propagation, pests/pathogens, or potential invasiveness) to improve conservation methods. Not all collections provide equal conservation value, however. While most collections of threatened plants can make important contributions to broader plant conservation initiatives through conservation-focused interpretation and education, not all collections provide direct conservation value at the research or reintroduction levels. Well-curated collections (living plant or germplasm) created from wild-collected, source-identified plant material can best support research and reintroduction applications for conservation.

Unfortunately, we do not currently understand the true conservation value of many of the collections included in this assessment. This must be resolved in the future by compiling and comparing accession-level data across living plant and germplasm collections to assess representation of natural populations in ex situ collections. We do know, however, that seed banks generally provide the highest conservation value in the most efficient manner, as they typically capture broad genetic diversity at relatively low costs over a long period of time. Seed banks can also provide plant material that is accessible and has direct, in situ conservation applications, to augment declining populations or reintroduce extirpated populations as needs arise. Therefore, there is an imperative to focus ex situ conservation efforts on building and strengthening seed bank collections for threatened species that produce orthodox seeds (able to be dried and stored). Currently in the United States, the collaborative network of the CPC is building secure, genetically

diverse seed bank collections for hundreds of the nation's most imperiled flora (CPC, 2012), and work like this is growing around the world.

For species with recalcitrant seeds or species that are no longer able to produce seeds at all, other types of collections can be well suited to provide adequate conservation value. This includes micropropagated and cryopreserved collections of plant tissue, which can efficiently capture relatively high genetic diversity and provide direct conservation applications. However, cryopreserved collections are more expensive than seed banks to maintain long term, and protocols for long-term cryopreservation have not yet been perfected for many threatened species (e.g., threatened oak species in the United States; Kramer & Pence, 2012). Well-documented, wild-collected living plant collections designed to capture high levels of genetic diversity (and curated to avoid hybridization or adaptation to cultivation) can also have high conservation value, particularly for species that do not produce orthodox seeds. Good examples of this are the palm and cycad collections maintained by the Montgomery Botanical Center based in Miami, Florida, U.S.A. (Namoff et al., 2010). For living plant collections, which typically contain lower genetic diversity than other types of ex situ collections, much-needed collaborations such as the broad-based North American Plant Collections Consortium (NAPCC) allow duplication and collection of key species and populations to occur in a strategic fashion (NAPCC, 2011).

Achieving the GSPC Target 8 by 2020 will require the continued integration of collections data, as well as targeted acquisition and germplasm distribution. As technology advances, including the ongoing development of collaborative online databases, we will be able to gain a better understanding of the source and diversity of and can work strategically to build conservation value in collections. The need for effective ex situ plant conservation and the role botanical collections can play are only going to grow in the future. It is imperative that the North American and global botanical communities work together to ensure an effective ex situ safety net is squarely in place for threatened plant species (BGCI U.S., 2012).

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INTERNATIONAL TRADE IN ENDANGERED PLANT SPECIES IN THE CONTEXT OF THE CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA AND THE GLOBAL STRATEGY FOR PLANT CONSERVATION[1]

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ABSTRACT

Several international treaties contain provisions to regulate and reduce negative impacts of international trade on endangered plant species. Focusing on the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Global Strategy for Plant Conservation (GSPC) of the Convention on Biological Diversity (CBD), this paper aims to elaborate existing and potential linkages between provisions and activities of these conventions. Based on an evaluation of CITES documentation, fields of potential synergies and/or joint activities between CITES and the GSPC are indicated.

Key words: Convention on Biological Diversity (CBD), Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Global Strategy for Plant Conservation (GSPC).

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) is an international agreement between governments aiming to ensure that trade in specimens of wild animals and plants does not threaten their survival. It entered in force on 1 July 1975 and, today, has 178 member parties (CITES, 2013a). Species covered by CITES are listed in three appendices. Appendix I comprises species threatened with extinction. CITES prohibits international trade in specimens of these species except for well-defined cases of noncommercial purposes. Appendix II includes species not necessarily threatened with extinction now, but in need of close controls to avoid detrimental trade. Appendix II also includes so-called "lookalike species" of species listed in the Appendices. Trade in Appendix II species is possible with CITES permits. Appendix III contains species based on a request by a Party to CITES that already regulates trade in that species and needs the cooperation of other countries to prevent detrimental exploitation (CITES, 2013b). The CITES Conference of the Parties (CoP) is the decision-making body of the Convention and comprises all its member States. Technical Committees like the CITES Plants Committee (PC) are established to provide, among others, scientific background for evaluations, discussions, and decisions at the CoPs. Terms of reference of the CITES PC include periodic reviews of listed species (in order to ensure appropriate categorization in the CITES Appendices) or the drafting of resolutions on plant issues for consideration by the CoPs (CITES, 2006).

THE GLOBAL STRATEGY FOR PLANT CONSERVATION OF THE CONVENTION ON BIOLOGICAL DIVERSITY

In 2002, the sixth CoP to the Convention on Biological Diversity (CBD) adopted, through Decision VI/9, the Global Strategy for Plant Conservation (GSPC). This strategy comprises 16 outcome-oriented targets to be reached by 2010 (CBD, 2002; Kiehn, 2002). After an evaluation of the implementation status of the targets in 2010, a consolidated and updated GSPC 2011–2020 with amended targets was adopted as Decision X/17 at the 10th CoP to the CBD

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in 2010 (CBD, 2011a, 2012). It is, however, widely accepted that its adequate implementation at a global level requires a major and proactive approach considering elements such as communication, capacity building, technology transfer, and financial support, among others (CBD, 2011b, 2013).

Convention on International Trade in Endangered Species of Wild Fauna and Flora and The Global Strategy for Plant Conservation

Already at the 13th Meeting of the CITES PC in Geneva, 2003, the CITES started to look into potential interactions between CITES and the GSPC. In the report of the working group WG5 of CITES PC13 (CITES, 2003), the responsibilities of CITES for the implementation of GSPC Target 11, "No species of wild flora endangered by international trade" (CBD, 2002, 2011c), are clearly expressed. It is noteworthy to mention here that, vice versa, the CBD in its 2009 Plant Conservation Report stated that "in essence, Target 11 forms the core business of CITES activities related to plants" (SCBD, 2009: 34). In addition to the focus on the GSPC Target 11, the working group WG5 of CITES PC13 also identified other GSPC targets where CITES activities are likely to provide useful contributions (CITES, 2003: 20; table 1). Since 2003, both the CITES CoPs and the CITES PC continued their evaluations of potential synergies and joint activities with the GSPC. The latest actions in this regard are documented by Decision 15.19 of CITES CoP 15 in Doha, Qatar, 2010. Directed to the PC and the Secretariat, this decision reads as follows: "The Plants Committee shall collaborate with the Global Strategy for Plant Conservation of the Convention on Biological Diversity, and with any processes established to develop the Strategy beyond 2010, provided it is related to CITES, as well as on other issues related to flora species included in the CITES Appendices, and the Secretariat shall communicate the contributions of CITES in the context of its Memorandum of Understanding with the CBD Secretariat" (CITES, 2010a). As a reaction to this decision, the 19th Meeting of the CITES PC prepared PC19 Doc. 8.4, which summarizes potential and real CITES contributions to the different targets of the updated GSPC 2011–2020 (CITES, 2011a). This document provides, in its Annex 1, a table that also can serve as basis for the discussion of such contributions (table 1). As a follow-up action, an intersessional working group was established at the 19th Meeting of the CITES PC (CITES, 2011e: 7) to draft a resolution related to the GSPC for discussion at the 20th Meeting of the CITES PC and for potential proposal as a resolution at the CoP 16 of CITES in 2013 (CITES, 2012).

What contributions does CITES offer to the GSPC (CBD) beyond Target 11?

Valuable contributions of CITES to Target 1 ("An online flora of all known plants") (CBD, 2011c) are checklists produced by CITES as part of its implementation processes. These checklists cover different plant groups that include several genera of the Orchidaceae (Roberts et al., 1995, 1997, 2001; Smith et al., 2006; Sieder et al., 2009), *Aloe* L. and *Pachypodium* Lindl., in the Xanthorrhoeaceae and Apocynaceae, respectively (Newton & Rowley, 2001; Lüthy, 2007), succulent Euphorbiaceae (Carter & Eggli, 2003), Cactaceae (Hunt, 1999), carnivorous plants (Von Arx et al., 2001), and bulbiferous plants (Davis et al., 1999). Meanwhile, most of these checklists are available online.

As regards to the GSPC Targets 2 ("An assessment of the conservation status of all known plant species, as far as possible, to guide conservation action") and 3 ("Information, research and associated outputs, and methods necessary to implement the Strategy developed and shared") (CBD, 2011c), the listing of a plant species in an Appendix of CITES is already an indication for a certain need of conservation action related to this taxon. In addition, all listing and amendment proposals to the Appendices must be accompanied by an in-depth evaluation of the conservation status. These data are available for uses outside of CITES as well. In this context, it is also important to notice that only the Appendix I listing reflects an actual threat with extinction, while the Appendix II listing is intended to counteract a potential threat, if exploitation through trade is not controlled to be sustainable, or if the listed species can be confused with another one (lookalike taxa) that requires CITES protection (CITES, 2013b). Table 1 of the Working Group report to CITES PC20 (CITES, 2012: 4–5) mentions a number of other processes routinely carried out in the context of the work of CITES, which are potentially useful for the implementation of GSPC Targets 2 and 3: nondetriment findings (NDFs), periodic reviews of the three Appendices, and reviews of significant trade. These processes not only reveal additional data about the conservation status of the taxa involved, but also have produced methodologies, which are likely to be applicable for the implementation of GSPC Targets 2 and 3. See, e.g., information documents prepared for the 18th CITES PC Meeting (CITES, 2009).

In the context of the GSPC Target 7 ("At least 75 per cent of known threatened plant species conserved

in situ"), the evaluation of the conservation status of taxa subject to listing and amendment proposals to the three CITES Appendices (cf. CITES, 2013b) normally includes data assessments on population level, with reference to distribution areas and habitats. These data can be helpful for in situ conservation programs for these species. This is exemplified in the Annexes 1 and 2 of CITES PC19 Doc. 14.3., related to Madagascan species of *Dalbergia* L. f. (Leguminosae) and *Diospyros* L. (Ebenaceae) (CITES, 2011b). Here, distribution and habitat data as well as the conservation status was assessed as the basis for potential listing proposals. In addition to these processes of data gathering and evaluation, efforts by CITES Parties to ensure sustainable use of CITES-listed species should also contribute to their survival in situ.

The CITES also contributes to Target 8 of the GSPC: "At least 75 per cent of threatened plant species in ex situ collections, preferably in the country of origin, and at least 20% available for recovery and restoration programmes" (CBD, 2011c). In the context of its operational work, CITES management authorities, in collaboration with the scientific authorities, have installed rescue and propagation centers for confiscated plants. These centers are often connected with botanical gardens and aim at the best possible curation for CITES-listed plants illegally transferred across borders, including options for ex situ propagation and potential repatriation of the material into the country of origin (and thus also of relevance in the context of GSPC Target 7). Cooperation between ex situ breeding operations and in situ activities are also addressed by CITES Resolution Conf. 13.9 ("Encouraging cooperation between Parties with ex situ breeding operations and those with in situ conservation programmes"). It urges:

"a) Parties to encourage ex situ operations . . . that artificially propagate Appendix-I plant species to seek cooperative measures that would support in situ conservation based on resources generated by those captive-breeding operations; and

b) Parties to encourage ex situ operations that breed or artificially propagate Appendix-I species within the range State, to support in situ conservation programmes; such support could consist of, inter alia, technical support, contribution of funds, exchange of specimens for reintroduction into the wild, capacity building and training, technology transfer, investment, infrastructure and other measures" (CITES, 2004).

Ex situ propagation is also explicitly encouraged by CITES Resolution Conf. 9.19 (Rev. CoP15) "Registration of nurseries that artificially propagate specimens of Appendix-I plant species for export purposes" (CITES, 2010b). Artificial propagation of plant species on demand on the markets is considered as a useful tool to reduce the pressure on populations of these species in the wild.

The sustainability of the intended use is one important criterion for NDFs of plant species listed in the CITES Appendix (cf. CITES, 2013b). This directly relates to the GSPC Target 12 ("All wild harvested plant-based products sourced sustainably") (CBD, 2011c). Such NDFs are preconditions for the issuing of CITES export permits and in some cases also for import permits. In addition, annotations to the three Appendices enable the regulation of certain target commodities, e.g., tropical timber or medicinal plant species.

Substantial contributions of CITES to the GSPC Target 13 ("Indigenous and local knowledge innovations and practices associated with plant resources, maintained or increased, as appropriate, to support customary use, sustainable livelihoods, local food security and health care") (CBD, 2011c) relate to plant species used in traditional medicine. In Resolution Conf. 10.19 (Rev. CoP14), CITES (2010c) gives clear guidelines for trade in such taxa, respecting and securing the rights and knowledge of indigenous peoples. Also, discussions about CITES and livelihood have taken place in the CITES Standing Committee, in order to promote traditional knowledge that ensures adequate CITES implementation, in particular related to the assessments needed for the preparation of NDFs (CITES, 2011d). The issue was also addressed at a symposium organized in May 2011 by Austria and the European Commission on "The relevance of Community-Based Natural Resource Management (CBNRM) to the conservation and sustainable use of CITES-listed species in exporting countries" (Abensperg-Traun et al., 2011). While the subjects dealt with there referred to the management of animals listed under CITES, the same principles could also be applied for CITES-listed plant species.

CITES has developed, encouraged, or commissioned the development of numerous training tools related to CITES-listed plants. This directly contributes to the GSPC Target 14 ("The importance of plant diversity and the need for its conservation incorporated into communication, education and public awareness programs") and GSPC Target 15 ("The number of trained people working with appropriate facilities sufficient according to national needs, to achieve the targets of this Strategy") (CITES, 2011a). CITES activities in this context include checklists,

slide shows, and training courses on CD-ROM (see, e.g., materials provided by the Royal Botanic Gardens Kew, <http://www.kew.org/conservation/cites-ind.html>) as well as training, Master's, and Ph.D. courses. The outreach of these courses is remarkable; e.g., the nine Master's degree courses in "management, access and conservation of species in trade: the international framework" at the Universidad Internacional de Andalucía in Baeza and the four associated Doctorate courses were attended by 235 individuals from 68 countries (CITES, 2011c). The latest development in this regard is the Virtual Campus, which is hosted by the Universidad Internacional de Andalucía in Baeza, Spain (<http://campusvirtual.unia.es/cites/>). This is still in development but already provides training material for NDFs and numerous resources.

Summary

The examples mentioned above are clear indications for the high potential of synergies between CITES activities related to plants and the GSPC. Undoubtedly, the main field of the GSPC where CITES provides valuable contributions is Target 11. However, CITES and the GSPC can share tools, scientific results, and methodologies in other areas like taxonomy, methods of assessing conservation status, or capacity building. Already existing interactions in these fields are encouraging but can be improved. Lastly, an intensified communication between national CITES and GSPC authorities, academic audiences, and NGOs, as well as between the Secretariats of CITES and the CBD, are essential cornerstones for successfully implementing joint collaborations of mutual benefit.

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APPLYING LESSONS FROM THE U.S. BOTANICAL CAPACITY ASSESSMENT PROJECT TO ACHIEVE 2020 GLOBAL STRATEGY FOR PLANT CONSERVATION TARGETS[1]

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ABSTRACT

Despite the fundamental role plant science plays in addressing global environmental issues, a recent survey of nearly 1600 members of the botanical community in the United States revealed a severe shortage in the nation's botanical capacity or resource capabilities that support the advancement of plant science. The survey and a subsequent published report detailed shortages of botanists at government agencies, a wave of upcoming retirements, and an alarming decline in botanical degree programs and course offerings at the nation's colleges and universities. Private sector organizations are filling gaps in botanical capacity created by declines in academic and government sectors. While this survey was carried out in the United States, its results are internationally relevant and applicable. These declines occur as the need for botanical capacity increases globally to address important plant conservation needs. Recognizing the critical situation facing the world's flora, the Convention on Biological Diversity (CBD) adopted the Global Strategy for Plant Conservation (GSPC) to halt the continuing loss of plant diversity. Our results illustrate the necessity of working across public and private sectors to ensure that botanical capacity is valued, supported, and utilized to achieve all 16 targets of the GSPC by 2020.

Key words: Botanical capacity, Global Partnership for Plant Conservation, Global Strategy for Plant Conservation, plant science education, research, and management, U.S.A.

The botanical community plays a critical role in researching, conserving, and sustainably managing the world's plant diversity and resources. Botanical capacity is the human, scientific, technological, organizational, institutional, and resource capabilities that support plant-based education and training, basic and applied research, and environmental monitoring and management. It is a critical component of efforts to address current and future challenges, such as climate change mitigation, land management and habitat restoration, invasive species control, and the conservation of rare species. Increased botanical capacity is necessary globally for achieving all 16 targets of the Global Strategy for Plant Conservation (GSPC) with the larger goal of halting the loss of plant diversity (Convention on Biological Diversity [CBD], 2010).

Despite the fundamental role botanical capacity plays in addressing key environmental challenges, it is often lacking in countries where plant diversity is highest (CBD, 2010). This includes developing tropical countries like Madagascar and Laos, where botanic gardens such as Missouri Botanical Garden and Royal Botanical Gardens, Kew, are working to build on-the-ground botanical capacity. Botanical capacity also appears to be eroding in many countries where it has historically been strongest, most notably the United Kingdom (Drea, 2011). This includes shortages of trained botanists at government agencies and declines in botanical degree programs and course offerings at colleges and universities. There is a clear need to better quantify and monitor botanical capacity in countries around the world because available information is largely anecdotal and often outdated. Without this information, it will be difficult to track trends in increasing or declining capacity and nearly impossible to achieve the GSPC targets by its 2020 deadline. This paper presents results from the first formal botanical capacity survey of government, academic, and private sectors across the United States, and connects findings and recommen-

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dations with ongoing efforts to reach the GSPC 2020 targets.

Assessing Botanical Capacity in the United States

To assess current botanical capacity as it applies to plant science research, education, and application in the United States, the Botanical Capacity Assessment Project was initiated in 2009 by the Chicago Botanic Garden, in partnership with Botanic Gardens Conservation International (BGCI) U.S. This cross-sector approach identified current strengths and areas where growth is needed by polling botanical professionals employed by universities, businesses, nonprofit organizations, and federal, state, and local governments.

We conducted an initial search of published and gray literature to synthesize all previous efforts to assess botanical capacity (education, training, research, application, and infrastructure) in the United States. Project staff then worked in consultation with members of an established advisory board and other individuals in the botanical community to develop, test, and carry out seven online surveys designed to capture information not available in the literature. Survey participants were from (1) federal government agencies; (2) state Natural Heritage Programs; (3) regional, state, county, or city government; (4) nonprofit organizations; (5) self-employed and for-profit sectors; (6) graduate students (master's and doctorate level); and (7) academic faculty.

Online surveys were widely advertised via print and electronic means, including through the Botanical Society of America and a range of plant science, conservation, and education listservs. The survey was open and publicly available during the summer of 2009. A total of 1569 individual survey responses were recorded, representing a diverse cross-section of the botanical community (Table 1). To our knowledge, it was the first time multiple sectors of the botanical community in the United States have been surveyed simultaneously. A workshop involving 30 stakeholders from government, academic, and private sectors was held at Chicago Botanic Garden in autumn 2009 to evaluate survey results and make recommendations for addressing critical gaps in botanical capacity. Key report findings are detailed below, and a full report (Kramer et al., 2010), including survey results and workshop recommendations, is available through the BGCI website, <http://www.bgci.org/usa/bcap>.

Education and Training

Botanical capacity in education and training is fundamental to achieving all targets of the GSPC, but is specifically related to Objective V and Targets 15 and 16 (CBD, 2010). The main task of Objective V and Targets 15 and 16 is to develop the capacities and public engagement necessary for halting the continuing loss of plant diversity, which involves increasing the number of trained people (Target 15), and strengthening the relationships among institutions, networks, and partnerships for plant conservation at national, regional, and international levels (Target 16). Unless we are able to build botanical capacity in education and training and ensure mechanisms are in place to monitor and sustain it over the long term, we will ultimately be unable to address the challenges posed by threats to plant diversity.

As early as 1952, a general decline in botany/plant-based curricula relative to general biology curricula at U.S. universities and colleges was noted (Greenfield, 1955), and by all indications, this trend continues today. This may be due in part to the widely recognized decline in organismal biology and taxonomy, including a decline in the support of natural history collections for both plants and animals (Gropp, 2003; Schwenk et al., 2009; Yoon, 2009) and is likely amplified by the phenomenon of what is termed as plant blindness, or a lack of awareness of plants in one's own environment (Wandersee & Schussler, 1999; Hershey, 2002). Research has shown that students have better recall for animals than plants (Schussler & Olzak, 2008), and science textbooks do little to help change this, as they describe and detail animals more so than plants in general (Link-Pérez et al., 2009). Much has been written about the need to update botanical curricula and education programs from pre-college (Daisey, 1996; Hershey, 1996; Goins, 2004; Enger, 2006; Hoot, 2009) to post-secondary education (Greenfield, 1955; Uno, 1988, 1994, 2002, 2007, 2009; Ewers, 2000; Cantino, 2004; Carter, 2004; Curtis & Bell, 2004; Sundberg, 2004; Senchina, 2008). Yet declines are ongoing and much remains to be done to ensure plant science is more broadly and effectively incorporated into the science and management curriculum of the United States.

It is possible to quantify some of the declines in botanical capacity in the academic sector using data from the National Science Foundation (Chaney et al., 1990; NSF, 1999, 2009). These data show that in 1988, 72% of the nation's top 50 most-funded universities offered advanced degree programs in botany. By 2009, more than half of these universities had eliminated their botany programs and many, if not all, had eliminated related courses. Likewise, data from the U.S. Department of Education, National

Center for Education Statistics (U.S. Department of Education, NCES, 2008) revealed that undergraduate degrees earned in botany declined by 50% between 2000 and 2008, whereas degrees awarded in general biology rose nearly 17% (Fig. 1).

In the United States, little quantitative information on the botanical capacity of the private sector is available, particularly with respect to for-profit businesses and self-employed and contracted individuals. In contrast, information on how botanic gardens and arboreta in the nonprofit sector contribute to botanical capacity through education and training is found in GardenSearch, the online database of the world's botanic gardens maintained by BGCI (2011). In the past century, GardenSearch reveals the number of botanic gardens in the United States has grown from fewer than 40 institutions to more than 450 (BGCI, 2011). This database identifies education programs at 152 U.S. botanical gardens, with more than 495 staff implementing these programs (at 92 botanic gardens that provided detailed employment statistics; see Table 2 for additional information on education efforts at botanic gardens).

Survey results helped quantify a growing gap in botanical capacity at the university level, specifically related to declines in botanical course offerings. Nearly 40% of the over 400 university faculty who completed the survey said botany courses in their department had been cut in the past five to 10 years. Those courses eliminated tended to be from among those required for employment as a botanist in the federal government. A majority of faculty and graduate student respondents were dissatisfied with botany courses offered by their college or university; field botany was identified as the most in-demand course to add to curricula (Fig. 2). Survey respondents also reported an inability to find adequately trained botanists to fill current open positions within government and nonprofit agencies, and they were generally dissatisfied with the botanical training of candidates and new hires (Sundberg et al., 2011). The elimination of botany degrees and courses across U.S. universities has a direct and severe impact on the scientific community's ability to meet the GSPC Targets 15 and 16.

Research and Management

Botanical capacity in research and management is also critical for achieving Objectives I and II of the GSPC, which ensures plant diversity is well understood, documented, and recognized (Objective I) and plant diversity is urgently and effectively conserved (Objective II; CBD, 2010). Specifically, Objective I,

Table 1. Percent of survey respondents (n = 1569 total respondents) shown by self-identified sector in which they work.

Sector	Percent of respondents
Federal government staff	34%
Academic faculty or administration	26%
Nonprofit organization staff	15%
Graduate students (Master's or Ph.D.)	13%
State or local government staff	6%
For-profit/self-employed staff	4%
State Natural Heritage Program staff	2%

Target 3 develops information, research, and the associated outputs necessary to implement the strategy. Objective II, Targets 4, 5, and 10 focus on conservation with at least 15% of each ecological region or vegetation type secured through effective management and/or restoration (Target 4); at least 75% of the most important areas for plant diversity of each ecological region protected with effective management in place for conserving plants and their genetic diversity (Target 5); and effective management plans in place to prevent new biological invasions and to manage important areas for plant diversity that are invaded (Target 10).

Nearly one third of all land in the United States is managed by the federal government, and in 2008, 1520 species (831 vascular plants, 374 vertebrates, 313 invertebrates, and two lichens) protected under the U.S. Endangered Species Act were found on federal lands in the United States. An additional 3069 species on federal lands were considered imperiled (2686 plants, 383 vertebrate taxa; Stein et al., 2008). Given these high numbers, it is important that botanists with specific botanical training and expertise are employed to help manage public lands and the threatened plants they support. However, it is currently not possible to identify the actual number of individuals with sufficient botanical training that are in place at federal government agencies. We do know that the workload and responsibilities of a federal botanist are often much greater than for federal wildlife biologists. For example, on California's National Forests each plant specialist is responsible for an average of 14 sensitive plant species, while animal specialists are each responsible for an average of only one sensitive animal species (Roberson, 2002). However, botanists are not compensated for this greater workload. In fact, they are paid much less than their counterparts: in March 2009, the U.S. Bureau of Labor Statistics (BLS) reported that federal government ecologists earned an average annual salary of $84,283;

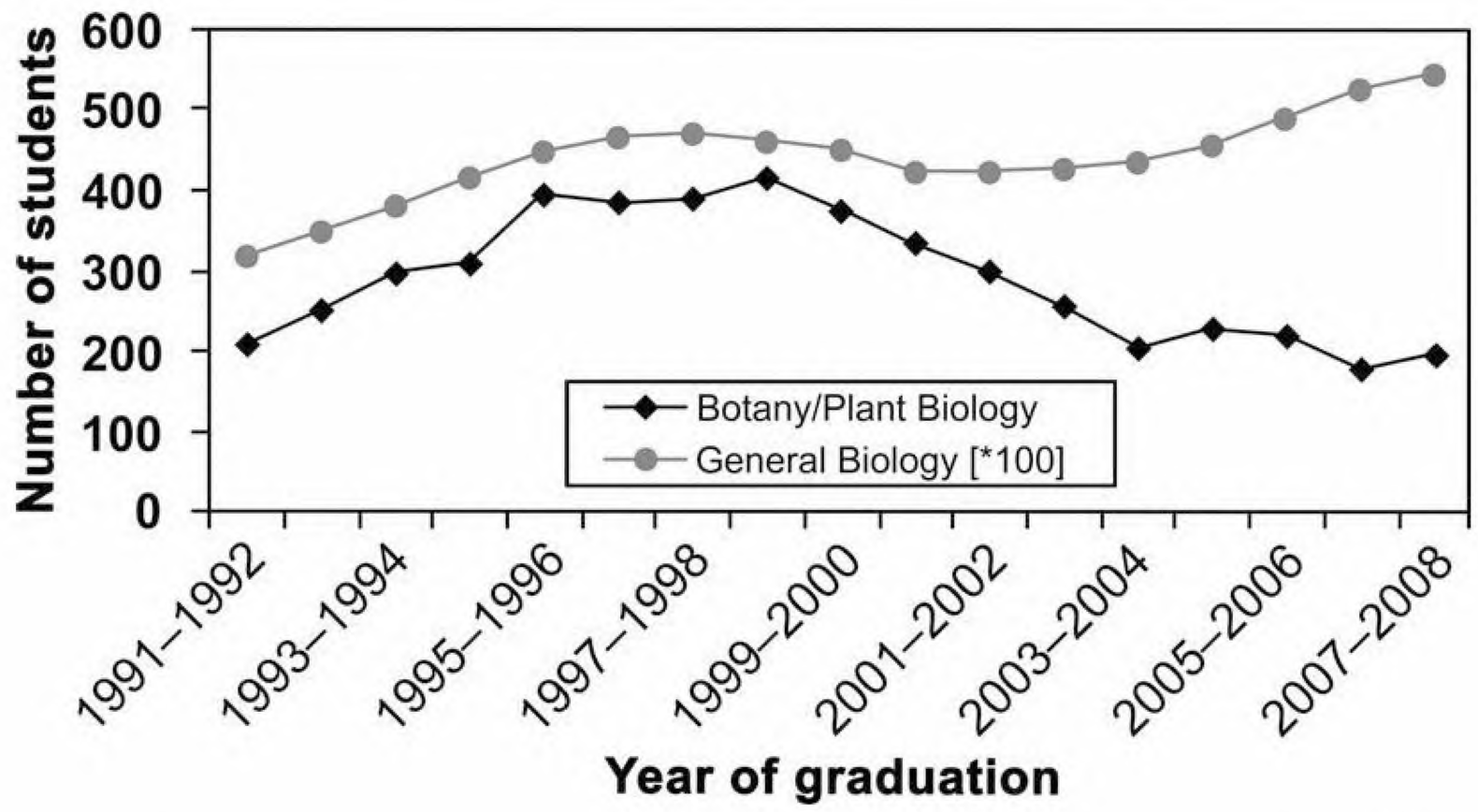


Figure 1. Comparison of undergraduate students graduating with a bachelor's degree in botany/plant biology versus a degree in general biology (data from the U.S. Department of Education, NCES, 2009). Note that numbers for general biology graduates are divided by 100 to facilitate viewing on a single graph.

zoologists, $116,908; and botanists, $72,792 (BLS, 2010).

Botanic gardens also provide important botanical research and management capacity, particularly when working in partnership with other sectors. For example, the Center for Plant Conservation (CPC) is a coordinated network of 38 botanical institutions dedicated to conserving and restoring imperiled native plants in the United States. The network collectively works with nearly 750 vulnerable species, including seed banking and restoration in the wild. Over the last 25 years, CPC participating institutions have banked nearly 22 million seeds of rare species, monitored ca. 2100 vulnerable plant sites, engaged in more than 202 reintroduction projects, are working to control invasive species at 94 wild sites, and conducted 47 other habitat restoration projects. Additional baseline data on botanical research and management capacity are provided by botanic gardens and arboreta in the United States in the BGCI's GardenSearch database. For example, in this database 41 gardens report an invasive species biology research program, and 73 report a plant conservation program (BGCI, 2011; Table 3).

Botanic gardens also amplify nationwide botanical capacity by working in partnership with other sectors. One example comes from the Seeds of Success program (SOS, 2010) led by the United States Department of the Interior, Bureau of Land Management. This national native seed collection and banking program is the result of a public-private collaboration involving numerous federal government agencies and private institutions (particularly botanic gardens) across the country. Since it began in 2001, this partnership has banked over 13,000 collections of native seeds at the Western Regional Plant Introduction Station (WRPIS) in Pullman, Washington, with back-up collections maintained by botanic gardens and partners across the country. This work is safeguarding native species against genetic erosion or even extinction, and providing opportunities for efficient and effective research and production of native plants in the United States.

Survey respondents were unanimous in selecting invasive plant species control as the top management issue requiring additional research, yet very few

Table 2. Education, training, and outreach summary statistics for U.S. botanic gardens and arboreta, as detailed in Botanic Gardens Conservation International's GardenSearch database (BGCI, 2011).

Education or training capacity	Summary for U.S. gardens (Nov. 2011)
Have an education program	152 gardens
Number of education staff	495 staff (n = 92 gardens reporting)
Education programs for K–12 students	64 gardens
Education programs at university level	45 gardens
Education programs for visitors	110 gardens
Number of volunteers engaged in activities	28,736 volunteers (n = 100 gardens reporting)

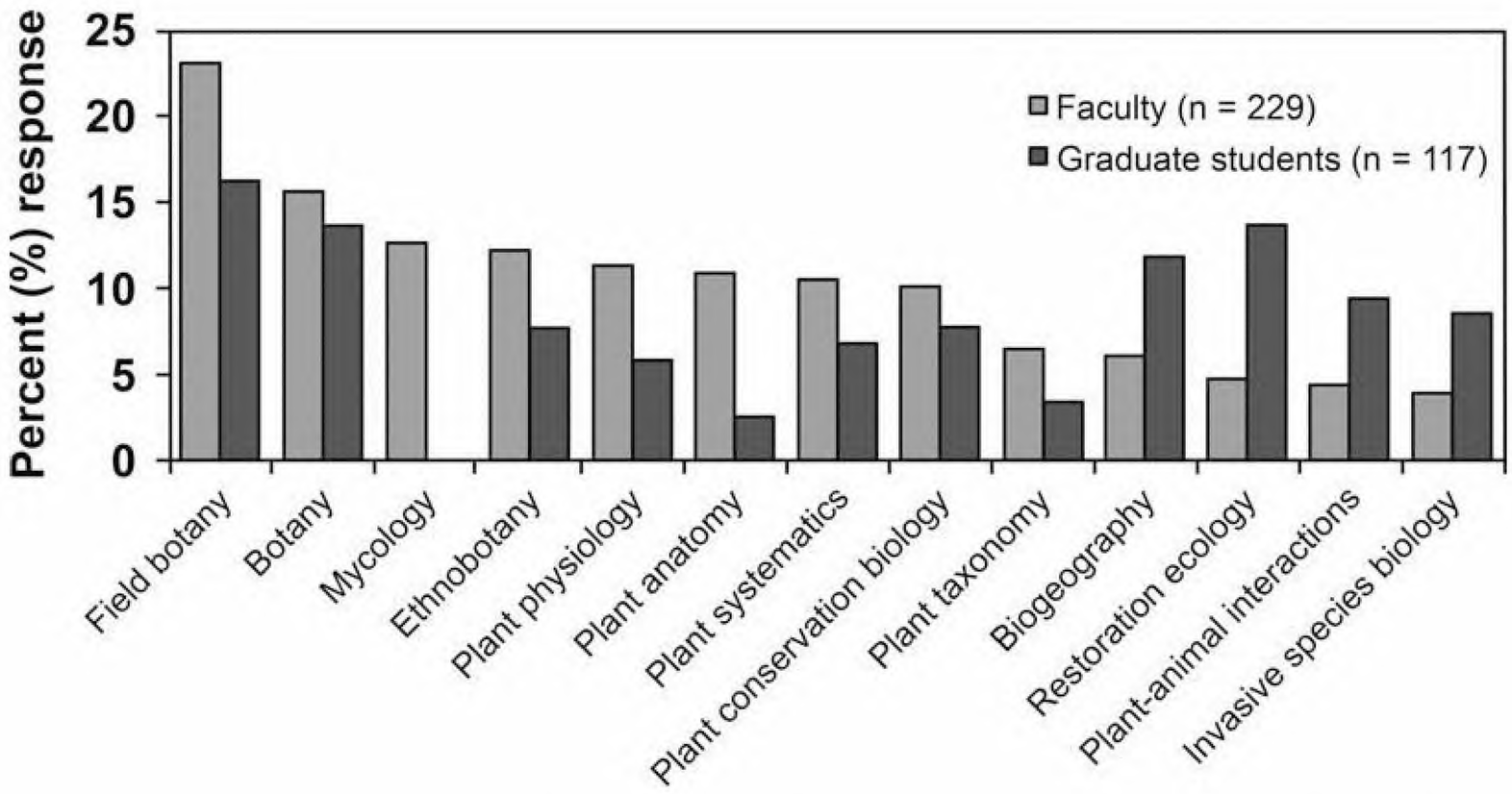


Figure 2. Plant science courses that faculty and graduate students responding to the survey felt should be added to their university's curriculum (Kramer et al., 2010).

faculty or graduate students reported undertaking research or offering courses that were applicable to invasive plant species control. This unmet demand for research on invasive species is a surprise, given that the United States currently spends more than $25 billion every year controlling invasive plant species (Pimentel et al., 2005; Pimentel, 2009), with costs expected to rise over the next decade.

Survey results documented severe shortages of management and research staff with botanical degrees, indicating government agencies currently lack the botanical capacity required to guide effective management of the nation's most critical biological resources. For example, in response to the question, "Do you think your agency has enough botanically trained staff to meet its current management/research needs?" Ninety-four percent of the 358 respondents in federal government agencies indicated that botany was the top employment area with shortages. These shortages occur throughout all federal and state government agencies, with some of the most significant found in agencies directly responsible for managing public lands.

Already critically lacking, botanical expertise at federal agencies will continue to decline over the next 15 years as more than half of the current workforce retires (Fig. 3). Because this decay in botanical infrastructure at government agencies is occurring in tandem with declines in botanical education and training opportunities at U.S. universities, it requires immediate attention. The private sector is filling many gaps in botanical education and research (for example, conducting research and teaching courses on invasive species biology and offering courses in field botany), but recommendations were made to support more sustainable partnerships among academic, private, and government sectors to ensure the private sector is able to continue filling these gaps in the future.

Recommendations to Address Gaps in Capacity

By filling gaps in education and training, and research and management, the botanical community will be better prepared to meet GSPC targets. Recommendations to address these gaps include the following seven (Kramer et al., 2010).

(1) Faculty and administration involved in college and university biology education should ensure plant science is appropriately incorporated in annual course offerings for undergraduate and graduate students to ensure they are employable both within and outside the academic sector. This includes

Table 3. Plant research and management summary statistics for U.S. botanic gardens and arboreta, as detailed in Botanic Gardens Conservation International's GardenSearch database (BGCI, 2011).

Research or management capacity	Summary for U.S. gardens (Nov. 2011)
Herbarium	45 gardens
Micropropagation/Tissue culture facility	18 gardens
Seed bank	32 gardens
Plant conservation program	73 gardens
Plant ecology research program	31 gardens
Invasive species biology research program	41 gardens
Restoration ecology research program	32 gardens
Plant systematics/Taxonomy research program	19 gardens
Floristics research program	17 gardens
Urban environment research program	24 gardens

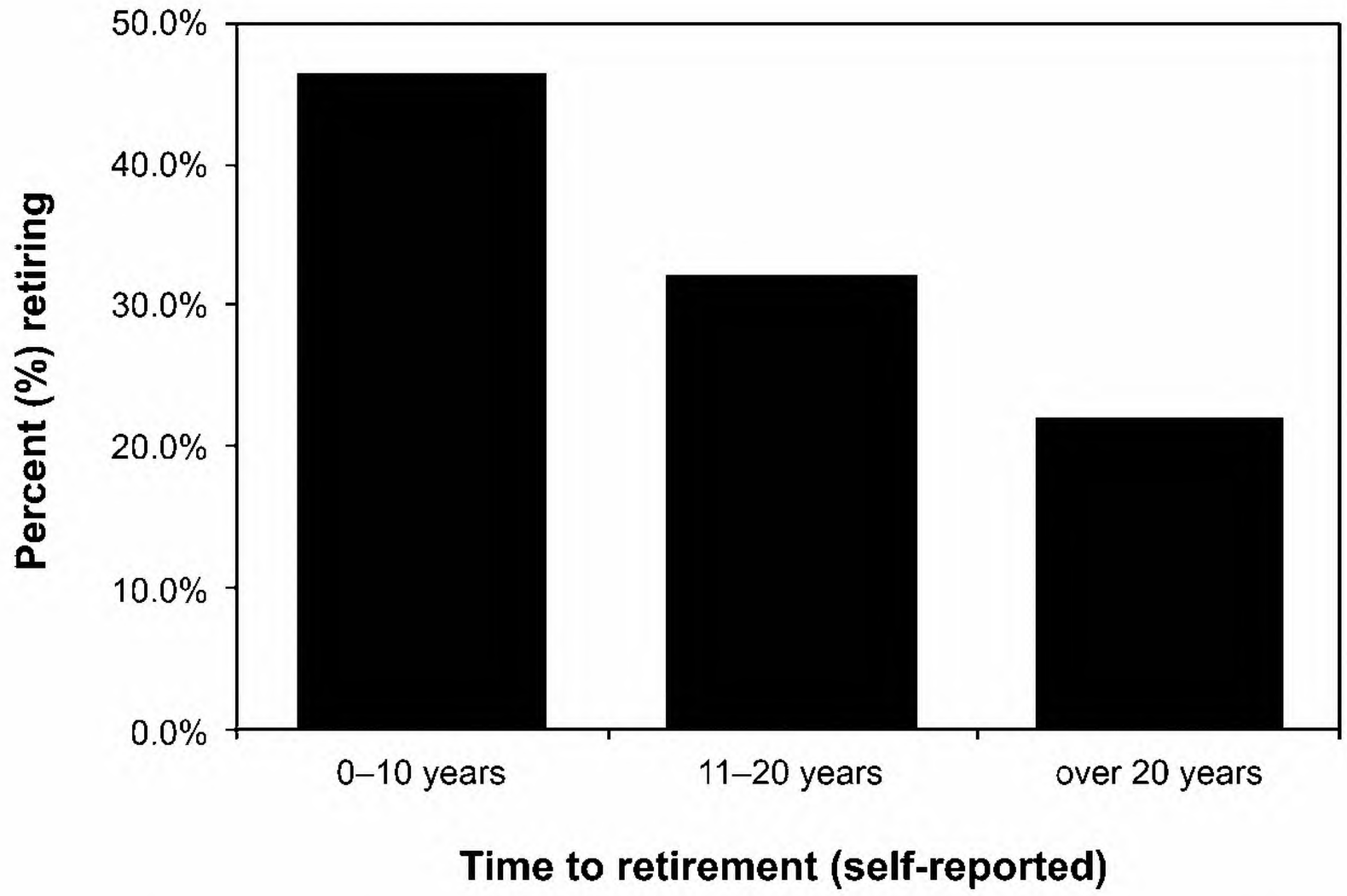


Figure 3. Retirement of survey respondents ($n = 147$) who are employed as federal botanists. There will be a significant need for a botanically trained workforce to fill the vacancies created by these retirements (Kramer et al., 2010).

offering courses that meet requirements for employment as a federal botanist (such as botany, plant anatomy, physiology, morphology, taxonomy and systematics, mycology, economic botany, ethnobotany, and other plant-specific courses), and encouraging interdisciplinary research programs to train students in both basic research and applied science.

(2) Faculty and administration at the nation's academic institutions should ensure plant science, including basic organismal expertise, is strongly represented within interdisciplinary departments, particularly as staff with botanical expertise retires in the coming decade. Accreditation bodies should develop recommendations and criteria for monitoring and evaluation to support adequate representation of botanical disciplines in biology departments and interdisciplinary study programs nationally.

(3) Nonprofit organizations play an increasingly critical role in filling gaps in botanical education and training. They contribute to course development and classroom education while providing practical experience, particularly for subjects that are most in demand for the nation's botanical workforce outside of academia. Because demand will increase in this area, nonprofit organizations should take strategic steps to increase their ability to fill this gap in capacity in this area. Leadership to recognize, support, and sustain the ability of nonprofit organizations to fill this role is needed from private foundations as well as academic and government sectors.

(4) Public and private funding should be directed to help all sectors close key gaps identified in plant science research that are directly linked to top needs and applications identified by this survey. This includes identified research needs in invasive species control, climate change mitigation and adaptation, habitat restoration, and the preservation of ecosystem services.

(5) Administrators and decision-makers at federal and state land management and research agencies should engage full-time staff botanists and work collaboratively with academic and private sector expert advisors in developing land-use plans, and in planning and implementing responses to key challenges (including climate change mitigation planning, habitat restoration, and invasive species control strategies).

(6) Federal and state land management and research agencies should provide support for full-time staff botanists to identify and prioritize plant-related issues, and ensure these priorities are clearly and consistently communicated to the academic and private sector to allow for effective and efficient action. Once identified and communicated, management and funding decisions in the private and public sectors should ensure that capacity and resources are focused on the highest priority issues (such as invasive species) and/or taxa (such as those most critically threatened).

(7) All federal land management and research agencies should ensure new hires have appropriate botanical training, and that monitoring and reporting mechanisms are in place to avoid a similar decay in botanical capacity in the future.

Application of Findings Outside the United States

Efforts to build botanical capacity in developing countries in support of the GSPC should consider identifying needs and monitoring botanical capacity so it can be built and sustained over the long term. Developed countries with established botanical capacity should develop processes to measure and monitor capacity over time, in order to define needs and take steps to prevent the loss of capacity or, in areas where capacity may already be lost, to rebuild it. All countries should work together to ensure that the need for public and private support of botanical capacity is widely understood and accepted.

Further Information

For full details on this assessment, and the results and recommendations that came from it, please visit <http://www.bgci.org/usa/bcap>, which contains free PDF copies of the full report (Kramer et al., 2010) executive summary, and recommendations.

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THE STATUS AND FUTURE OF ORCHID CONSERVATION IN NORTH AMERICA[1]

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ABSTRACT

The status and trends of issues related to the conservation of orchids native to the United States, Canada, and Greenland are considered. We focus on nine of the 16 Targets of the Global Strategy for Plant Conservation (GSPC). The first two targets, which all other targets rely upon, appear to have been adequately achieved, in addition to Target 11. Limited progress has been made on six other GSPC targets. Three case studies of efforts to conserve the native threatened orchids, *Platanthera leucophaea* (Nutt.) Lindl., *Isotria medeoloides* (Pursh) Raf., and *Tolumnia bahamensis* (Nash) Braem, are presented to demonstrate the difficulties as well as the issues associated with effective conservation. We describe our efforts to establish an international program to conserve all native orchids in the United States and Canada. The North American Orchid Conservation Center (NAOCC) is an internationally focused effort that is based on public-private partnerships. The goal of NAOCC is to conserve the genetic diversity of all native orchids through efforts to develop an international collection of seeds and orchid fungi. The NAOCC also focuses on the cultivation of all native orchids in an international network of botanic gardens, and they partner with private and public landowners to develop techniques to conserve and restore all native orchid species.

Key words: Endangered species, Global Strategy for Plant Conservation (GSPC), North American Orchid Conservation Center (NAOCC), Orchidaceae, restoration.

Beautiful, diverse, and often bearing large and showy flowers, orchids are an ancient plant family that has evolved an amazing array of bizarre flower types, unique pollination syndromes, and complex symbiotic interactions with animals and fungi. In the plant world, orchids reign supreme as about 10% of all flowering plant species are members of the Orchidaceae. No other plant family can match the peculiar array of evolutionary features that orchids collectively possess. Along with the Asteraceae, the Orchidaceae has more species, estimated to be between 20,000 and 35,000 taxa (Cribb et al., 2003), than any other family of flowering plants, and individual orchid species are often rare in nature, occurring in restricted and specific niches and habitats. Collectors prize orchids for their seemingly infinite variety of showy flowers; scientists have long been fascinated by the relationships between the plants and their pollinators and other symbionts.

Today, orchids have taken on even greater significance. Due to their interconnectedness with the species around them, orchids, highly sensitive to habitat change, are among the first casualties from environmental degradation. Most orchid genera contain threatened or endangered species (Swarts & Dixon, 2009). Orchids are found throughout North America, and many of the approximately 210 species found north of Mexico are threatened, endangered, or extirpated in at least part of their ranges because of habitat loss and alteration. Most North American orchids are terrestrial. Globally, terrestrial orchids make up only one third of orchid species with the other two thirds being epiphytes and lithophytes. However, terrestrial herbaceous perennials are disproportionately represented in the extinct plant species listed by The World Conservation Union (IUCN, 1999). Consequently, terrestrial orchids are likely subject to a greater extinction risk than epiphytes, particularly in response to current climate changes.

Much of orchids' sensitivity to habitat change likely can be traced to their dependence on two, often

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very specific, types of symbiotic associations. Orchids' relationships with specific pollinators have been a subject of interest since before Darwin, but more recently orchid dependence on mycorrhizal fungi has also received substantial research attention (Waterman & Bidartondo, 2008). Identification of the fungi on which orchids depend requires DNA sequencing and analysis, but it is clear at this point that some orchids are dependent upon fungi that are free living in the soil, while others associate with fungi that are also connected to other plants, especially trees. As habitats change, the fungal community changes, and orchids may lose fungi upon which they depend for their survival.

As popular, desirable, and charismatic subjects for cultivation, orchids face another serious threat. Like precious gems, the most unique and rare orchids are sought by the most enthusiastic collectors. As word spreads about the location of a rare orchid, more and more demand is placed on already fragile populations. Unfortunately, without efforts to cultivate the symbiotic fungi, most of these plants are doomed in cultivation. Due to the combination of habitat loss and poaching, many orchid species, which were once widespread, are now found in small, ecologically fragile, fragmented populations. The majority of orchids are represented globally by tropical epiphytes, but temperate zone terrestrials make up a significant proportion (approximately 28%; Gravendeel et al., 2004) and conservation of terrestrial species has proven to be especially challenging (e.g., Stewart & Hicks, 2010). No orchid has ever been delisted, though one, *Isotria medeoloides* (Pursh) Raf., was upgraded from endangered to threatened in 1994 (U.S. Fish and Wildlife Service, 1994) after extensive directed searching uncovered new populations. A comprehensive holistic approach to species conservation has to be fully realized in conservation and restoration plans.

The orchid flora of North America represents an important scientific challenge for conservation biologists. Unlike many other plant species, where significant efforts are often employed to cultivate and reintroduce rare plants and to store germplasm, the majority of organizations that identify and protect orchids on public and private lands rely solely on habitat conservation for management. This conservation strategy has largely been dictated by the unique aspects of orchid biology that make them not amenable to standard plant conservation techniques. We propose a model of centralized but integrated orchid conservation that can provide one-stop shopping for agencies and organizations responsible for and actively participating in efforts to conserve native orchids.

We begin by identifying successes and major gaps in conservation strategies for North American native orchids by addressing nine of the 16 targets of the 2011–2020 Global Strategy for Plant Conservation (GSPC) in relation to the conservation of orchid species native to the United States, Canada, and Greenland. GSPC targets 4, 5, 6, 9, 10, 12, and 13 do not apply directly to native North American orchid species. We then propose a centralized North American Orchid Conservation Center (NAOCC) that addresses each deficiency.

Global Strategy of Plant Conservation Targets

target 1, an online flora of all known plants

A total of 210 orchid species are native to the United States, Canada, and Greenland (see Table 1), including one described as recently as 2007, as *Platanthera yosemitensis* Colwell, Sheviak & P. E. Moore (Colwell et al., 2007). The novel orchid list is a compilation of species from Kartesz (1994), the Flora of North America (Romero-González et al., 2002), Brown (2009), and NatureServe Explorer (NatureServe, 2011), and each name is accepted by The Plant List (<http://www.thePlantList.org>) and the World Checklist of Selected Plant Families (WCSP, 2011). Additionally, 135 orchid species are native to Puerto Rico and the Virgin Islands (Acevedo-Rodríguez & Strong, 2007), but of these species only those that extend into the mainland are treated here.

The 210 described species (Table 1) are distributed among 66 genera (Table 2), with 49 genera (74%) represented by only one or two species and a few genera being represented by more than three species (e.g., *Platanthera* Rich. with 35 species, *Spiranthes* Rich. with 23 species). While there are always questions of whether taxa should be split or lumped and questions about the treatment of hybrids, relationships between most genera in the Orchidaceae are well established (e.g., Górniak et al., 2010).

Native orchid species are found in all 50 states within the United States and all 10 provinces and three territories of Canada. On average, there are 40 native species per state, with Hawaii having the fewest native species (three) and Florida with the most (106). Other species-rich areas include the states along the East Coast associated with the Appalachian Mountains, especially North Carolina (67 species), Virginia (59 species), and New York (57 species). Of the Canadian provinces, Prince Edward Island and Ontario have an especially diverse orchid assemblage (59 and 58 species, respectively). All

Table 1. The 210 native orchid species of the United States, Canada, and Greenland, including conservation assessments, legal protections, and the number of botanic gardens holding ex situ collections. This list is a compilation of species from Kartesz (1994), the Flora of North America (Romero-González et al., 2002), Brown (2009), and NatureServe Explorer (NatureServe, 2011).

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Anoectochilus sandvicensis Lindl.	G3; S3	Vulnerable				1
Aplectrum hyemale (Muhl. ex Willd.) Nutt.	G5; SH, S1-S5, SNR			Endangered		11
Arethusa bulbosa L.	G4; SX, SH, S1-S4, SNR			Endangered		0
Basiphyllaea corallicola (Small) Ames	G2; S1			Endangered		0
Beloglottis costaricensis (Rchb. f.) Schltr.	G4; S1*			Endangered		0
Bletia patula Hook.	G4; SH					5
Bletia purpurea (Lam.) DC.	G5; S3			Threatened		17
Brassia caudata (L.) Lindl.	G3; SX			Endangered		37
Bulbophyllum pachyrachis (A. Rich.) Griseb.	G4; SX					0
Calopogon barbatus (Walter) Ames	G4; S1-S3, SNR					1
Calopogon multiflorus Lindl.	G2; SH, S1-S3			Endangered		0
Calopogon oklahomensis D. H. Goldman	G3; SH, S1, S2, SNR					0
Calopogon pallidus Chapm.	G4; S1-S5, SNR					2
Calopogon tuberosus (L.) Britton, Sterns & Poggenb.	G5; SX, S1-S4, SNR			Endangered		16
Calypso bulbosa (L.) Oakes	G5; SH, S1-S5, SNR			Endangered		8
Camaridium vestitum (Sw.) Lindl.	G4; S1*					5*
Campylocentrum pachyrrhizum (Rchb. f.) Rolfe	G4; S1			Endangered		1
Cephalanthera austiniae (A. Gray) A. Heller	G4; S2, S3, SNR				Threatened	1
Cleistesiopsis bifaria (Fernald) Pansarin & F. Barros	G4; S1-S4, SNR*					3*
Cleistesiopsis divaricata (L.) Pansarin & F. Barros	G4; SX, S1, S3, S4, SNR*			Endangered*		1
Cleistesiopsis oricamporum P. M. Br.	GNR; S2					0
Corallorhiza bentleyi Freudenst.	G1; S1					0
Corallorhiza maculata (Raf.) Raf.	G5; SH, S1-S4, SNR			Endangered		12
Corallorhiza mertensiana Bong.	G4; S2, S3, S5, SU, SNR					1
Corallorhiza odontorhiza (Willd.) Nutt.	G5; SH, S1-S5, SNR			Endangered		2
Corallorhiza striata Lindl.	G5; SH, S1-S4, SNR			Endangered		0
Corallorhiza trifida Châtel.	G5; S1-S5, SNR			Endangered		2
Corallorhiza wisteriana Conrad	G5; SX, SH, S1-S5, SNR			Endangered		2
Cranichis muscosa Sw.	G4; S1			Endangered		2
Cyclopogon cranichoides (Griseb.) Schltr.	G4; SNR*					0
Cyclopogon elatus (Sw.) Schltr.	G4; SH*			Endangered		4*
Cypripedium acaule Aiton	G5; S1, S3-S5, SNR			Endangered		22

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Cypripedium arietinum R. Br.	G3; SH, S1-S3			Endangered		1
Cypripedium californicum A. Gray	G3; S3					7
Cypripedium candidum Muhl. ex Willd.	G4; SX, SH, S1-S3, SNR			Endangered	Endangered	10
Cypripedium fasciculatum Kellogg ex S. Watson	G4; S1-S3					2
Cypripedium guttatum Sw.	G5; S2, SNR					7
Cypripedium kentuckiense C. F. Reed	G3; S1-S3			Endangered		14
Cypripedium montanum Douglas ex Lindl.	G4; S1-S4, SNR					3
Cypripedium parviflorum Salisb.	G5; SH, S1-S4, SNR			Endangered		12
Cypripedium passerinum Richardson	G4; S1-S4, SNR					2
Cypripedium reginae Walter	G4; SX, S1-S4, SU, SNR, SNA			Endangered		33
Cypripedium yatabeanum Makino	G4; SNR*					1
Cyrtopodium punctatum (L.) Lindl.	G5; S1			Endangered		22
Dactylorhiza aristata (Fisch. ex Lindl.) Soó	G4; S4					0
Dactylorhiza viridis (L.) R. M. Bateman, Pridgeon & M. W. Chase	G5; SX, SH, S1-S5, SNR*			Endangered		11*
Dendrophylax lindenii (Lindl.) Benth. ex Rolfe	G3; S2*			Endangered		7*
Dendrophylax porrectus (Rchb. f.) Carlsward & Whitten	GU; SNR*					0
Dichromanthus cinnabarinus (La Llave & Lex.) Garay	G5; SNR*					2
Dichromanthus michuacanus (La Llave & Lex.) Salazar & Soto Arenas	G4; S3, SNR*					0
Eltroplectris calcarata (Sw.) Garay & H. R. Sweet	G4; S1			Endangered		1
Encyclia tampensis (Lindl.) Small	G4; SNR					23
Epidendrum amphistomum A. Rich.	GNR; S3			Endangered		0
Epidendrum anceps Jacq.						10
Epidendrum blancheanum Urb.	G4; SX			Endangered*		1*
Epidendrum floridense Hágsater						5
Epidendrum magnoliae Muhl.	G4; S2, S3, SNR*					4*
Epidendrum nocturnum Jacq.	G4; S2			Endangered		25
Epidendrum rigidum Jacq.	G4; S3			Endangered		19
Epidendrum strobiliferum Rchb. f.	G4; S1			Endangered		1
Epipactis gigantea Douglas ex Hook.	G4; S1-S3, SU, SNR				Special Concern	37
Eulophia alta (L.) Fawc. & Rendle	G4; S4					6
Eulophia ecristata (Fernald) Ames	G2; S1, S2*			Endangered		0

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Galeandra beyrichii Rchb. f.	G4; SNR					0
Galeandra bicarinata G. A. Romero & P. M. Br.	G1; S1			Endangered		0
Galearis spectabilis (L.) Raf.	G5; S1-S5, SNR			Endangered		4
Goodyera oblongifolia Raf.	G5; S1-S5, SNR			Endangered		9
Goodyera pubescens (Willd.) R. Br.	G5; S1-S5, SNR			Endangered		27
Goodyera repens (L.) R. Br.	G5; SH, S1-S5, SNR			Endangered		14
Goodyera tesselata Lodd.	G5; SX, SH, S1-S5, SU, SNR			Endangered		3
Govenia floridana P. M. Br.				Endangered		0
Habenaria distans Griseb.	G5; S1			Endangered		1
Habenaria floribunda Lindl.	G4; SNR*					2*
Habenaria quinqueseta (Michx.) Sw.	G4; S1, SNR					1
Habenaria repens Nutt.	G5; S1-S3, SNR					4
Hammarbya paludosa (L.) Kuntze	G4; S1-S3, SNR*			Endangered*		2
Heterotaxis sessilis (Sw.) F. Barros	G4; S1*					18*
Hexalectris grandiflora (A. Rich. & Galeotti) L. O. Williams	G4; S2					2
Hexalectris nitida L. O. Williams	G3; S1, S3			Endangered		2
Hexalectris revoluta Correll	G1; S1, SNR					0
Hexalectris spicata (Walter) Barnhart	G5; SH, S1-S4, SNR			Endangered		3
Hexalectris warnockii Ames & Correll	G2; S1, S2					0
Ionopsis utricularioides (Sw.) Lindl.	G4; S1			Endangered		10
Isotria medeoloides (Pursh) Raf.	G2; SX, SH, S1, S2	Threatened		Endangered	Endangered	1
Isotria verticillata (Muehl. ex Willd.) Raf.	G5; SX, S1-S5, SNR			Endangered	Endangered	5
Lepanthopsis melanantha (Rchb. f.) Ames	G3; SH			Endangered		1
Liparis hawaiensis H. Mann	G3; S3					3
Liparis liliifolia (L.) Rich. ex Lindl.	G5; SX, S1-S5, SNR			Endangered	Endangered	4
Liparis loeselii (L.) Rich.	G5; SX, SH, S1-S5, SNR			Endangered		8
Liparis nervosa (Thunb.) Lindl.	G4; S2			Endangered*		10
Macradenia lutescens R. Br.	G4; SH			Endangered		0
Malaxis abieticola Salazar & Soto Arenas	G4; S1, S3*					0
Malaxis bayardii Fernald	G1; SH, S1, SU			Endangered		0
Malaxis brachystachys (Rchb. f.) Kuntze	G4; S3, S4*					0
Malaxis macrostachya (Lex.) Kuntze	G4; SNR, SNA					3*
Malaxis monophyllos (L.) Sw.	G4; SH, S1-S4, SNR*			Endangered*		1
Malaxis porphyrea (Ridl.) Kuntze	G4; S2, SNR					0

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Malaxis spicata Sw.	G4; S1-S3, SNR					0
Malaxis unifolia Michx.	G5; S1-S5, SX, SNR			Endangered		2
Malaxis wendtii Salazar	G2; S1					0
Mesadenus lucayanus (Britton) Schltr.	G4; S1, S2*			Endangered		1*
Microthelys rubrocallosa (B. L. Rob. & Greenm.) Garay	GNR; S1					0
Neottia auriculata (Wiegand) Szlach.	G3; S1-S3, SNR*			Endangered		0
Neottia banksiana (Lindl.) Rchb. f.	G4; S1-S4, SNR*					4*
Neottia bifolia (Raf.) Baumbach	G4; S1-S4, SNR*			Endangered*		5*
Neottia borealis (Morong) Szlach.	G4; SH, S1-S4, SNR*					0
Neottia convallarioides (Sw.) Rich.	G5; S1-S4, SNR*					0
Neottia cordata (L.) Rich.	G5; SH, S1-S5, SNR*			Endangered*		1
Neottia smallii (Wiegand) Szlach.	G4; S1-S4*			Endangered*		0
Oncidium ensatum Lindl.	GNR; S1			Endangered*		9*
Pelexia adnata (Sw.) Poit. ex Rich.	G5; S1			Endangered		1
Peristylus holochila (Hillebr.) N. Hallé	G1; S1*	Endangered*				3*
Piperia candida Rand. Morgan & Ackerman	G3; S2, S3, SNR					0
Piperia colemanii Rand.Morgan & Glic.	G3; S3					0
Piperia cooperi (S. Watson) Rydb.	G4; S3					0
Piperia dilatata (Pursh) Szlach. & Rutk.	G5; SH, S1-S5, SU, SNR*					5*
Piperia elegans (Lindl.) Rydb.	G4; S3, S4, SNR					1
Piperia elongata Rydb.	G4; S3, S4, SNR					0
Piperia leptopetala Rydb.	G3; S3					0
Piperia transversa Suksd.	G4; S3, S4, SNR					0
Piperia unalascensis (Spreng.) Rydb.	G5; S1-S5, SNR					0
Piperia yadonii Rand. Morgan & Ackerman	G2; S2	Endangered				0
Platanthera aquilonis Sheviak	G5; SX, S1-S5, SU, SNR					3
Platanthera blephariglottis (Willd.) Lindl.	G4; S1-S4, SNR			Endangered		4
Platanthera brevifolia (Greene) Senghas	G4; SNR					0
Platanthera chapmanii (Small) Luer	G2; S1, SH, SNR					1
Platanthera chorisiana (Cham.) Rchb. f.	G3; S2-S4			Threatened		2
Platanthera ciliaris (L.) Lindl.	G5; SX, SH, S1-S4, SNR			Endangered		5
Platanthera clavellata (Michx.) Luer	G5; SH, S1-S5, SU, SNR					2
Platanthera convallariifolia (Fisch. ex Lindl.) Lindl.						0

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Platanthera cristata (Michx.) Lindl.	G5; S1-S4, SX, SNR			Endangered		0
Platanthera flava (L.) Lindl.	G4; SX, S1-S4, SU, SNR			Endangered		1
Platanthera grandiflora (Bigelow) Lindl.	G5; SX, S1-S4, SNR			Endangered		3
Platanthera hookeri (Torr.) Lindl.	G4; SX, S1-S4, SH, SNR			Endangered		2
Platanthera huronensis Lindl.	G5; S1-S5, SU, SNR*					3
Platanthera hyperborea (L.) Lindl.	G5; S4			Endangered		5
Platanthera integra (Nutt.) A. Gray ex L. C. Beck	G3; S1-S3, SNR			Endangered		0
Platanthera integrilabia (Correll) Luer	G2; SH, S1-S3, SU		Candidate	Endangered		1
Platanthera lacera (Michx.) G. Don	G5; S1-S5, SNR					7
Platanthera leucophaea (Nutt.) Lindl.	G2; SX, SH, S1, S2		Threatened	Endangered	Endangered	2
Platanthera limosa Lindl.	G4; S4, SNR					0
Platanthera nivea (Nutt.) Luer	G5; SH, S1-S3, SNR			Endangered		1
Platanthera obtusata (Banks ex Pursh) Lindl.	G5; S1-S5, SNR			Vulnerable		1
Platanthera orbiculata (Pursh) Lindl.	G5; SX, SH, S1-S4, SNR			Endangered		1
Platanthera pallida P. M. Br.	GNA; SU, SNA, SNR*					0
Platanthera peramoena A. Gray	G5; SX, S1-S4, SNR			Endangered		1
Platanthera praeclara Sheviak & M. L. Bowles	G3; SH, S1-S3	Endangered	Threatened	Endangered	Endangered	1
Platanthera psycodes (L.) Lindl.	G5; SX, SH, S1-S5, SNR			Endangered		2
Platanthera purpurascens (Rydb.) Sheviak & W. F. Jenn.						0
Platanthera rotundifolia (Banks ex Pursh) Lindl.	G5; SX, SH, S1-S5, SNR*			Endangered*		1
Platanthera shriveri P. M. Br.	G1; S1, SNR					0
Platanthera sparsiflora (S. Watson) Schltr.	G4; S1, SNR			Sensitive		0
Platanthera stricta Lindl.	G5; S1-S5, SNR					4*
Platanthera tescamnis Sheviak & W. F. Jenn.						0
Platanthera tipuloides (L. f.) Lindl.	G4; S2					0
Platanthera yosemitensis Colwell, Sheviak & P. E. Moore	G2; S2					0
Platanthera zothecina (L. C. Higgins & S. L. Welsh) Kartesz & Gandhi	G2; S1, S2					0
Platythelys querceticola (Lindl.) Garay	G4; S1, SNR					0
Platythelys sagraeana (A. Rich.) Garay						0
Pogonia ophioglossoides (L.) Ker Gawl.	G5; SX, SU, S1-S5, SNR			Endangered		17
Polystachya concreta (Jacq.) Garay & H. R. Sweet	G4; S3			Endangered		13
Ponthieva brittoniae Ames	G3; S1			Endangered		1

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Ponthieva racemosa (Walter) C. Mohr	G4; S1-S3, SNR			Endangered		4
Prescottia oligantha (Sw.) Lindl.	G4; S1					1
Prosthechea boothiana (Lindl.) W. E. Higgins	G4; S1*					6*
Prosthechea cochleata (L.) W. E. Higgins	G4; S3*					65*
Prosthechea pygmaea (Hook.) W. E. Higgins	G4; S1*			Endangered		9*
Pseudorchis albida (L.) Á. Löve & D. Löve	G5; S3, SNR*					3
Sacoila lanceolata (Aubl.) Garay	G4; S3*			Threatened*		8*
Sacoila squamulosa (Kunth) Garay						0
Schiedeella arizonica P. M. Br.	GNR; S3, S4, SNR					0
Schiedeella confusa (Garay) Espejo & López-Ferr.	G3; SNR*					0
Spiranthes brevilabris Lindl.	G1; S1, SNR			Endangered		0
Spiranthes casei Catling & Cruise	G4; S1-S4, SNR			Endangered		0
Spiranthes cernua (L.) Rich.	G5; S1-S5, SU, SNR			Vulnerable		28
Spiranthes delitescens Sheviak	G1; S1		Endangered	Endangered		1
Spiranthes diluvialis Sheviak	G2; S1, S2	Threatened		Endangered		5
Spiranthes eatonii Ames ex P. M. Br.	G3; SH, S1-S3, SNR					0
Spiranthes infernalis Sheviak	G1; S1					0
Spiranthes lacera (Raf.) Raf.	G5; S1-S5, SNR			Threatened		5
Spiranthes laciniata (Small) Ames	G4; S1-S4, SU, SNR			Endangered		0
Spiranthes longilabris Lindl.	G3; SH, S1-S3, SNR			Threatened		0
Spiranthes lucida (H. H. Eaton) Ames	G5; SX, SH, S1-S5, SNR			Endangered		2
Spiranthes magnicamporum Sheviak	G4; SX, S1-S4, SNR			Endangered		2
Spiranthes ochroleuca (Rydb.) Rydb.	G4; SH, S1-S3, S5, SNR			Endangered		2
Spiranthes odorata (Nutt.) Lindl.	G5; SH, S1-S4, SU, SNR			Endangered		15
Spiranthes ovalis Lindl.	G5; SH, S1-S5, SNR			Endangered		3
Spiranthes parksii Correll	G3; S3		Endangered	Endangered		2
Spiranthes porrifolia Lindl.	G4; S1, S2, S4, SNR			Sensitive		3
Spiranthes praecox (Walter) S. Watson	G5; SH, S1-S4, SU					1
Spiranthes romanzoffiana Cham.	G5; SH, S1-S5, SU, SNR			Endangered		5
Spiranthes sylvatica P. M. Br.	GNR; S1					0
Spiranthes torta (Thunb.) Garay & H. R. Sweet	G4; S1*			Endangered		0
Spiranthes tuberosa Raf.	G5; SH, S1-S5, SNR			Endangered		4
Spiranthes vernalis Engelm. & A. Gray	G5; S1-S5, SNR			Endangered		5
Stelis gelida (Lindl.) Pridgeon & M. W. Chase	G5; S1*			Endangered*		3
Tipularia discolor (Pursh) Nutt.	G4; S1, S3-S5, SNR			Endangered		15

Table 1. Continued.

Species	NatureServe conservation status ranks[a]	IUCN 2011 Red List[b]	U.S. Endangered Species Act[c]	U.S. State conservation listing[d]	Canada's Species At Risk Act[e]	Number of botanic gardens where present[f]
Tolumnia bahamensis (Nash ex Britton & Millsp.) Braem	G3; S1			Endangered		5
Trichocentrum undulatum (Sw.) Ackerman & M. W. Chase	G4; S1*			Endangered*		1
Triphora amazonica Schltr.				Endangered		0
Triphora craigheadii Luer	G1; S1			Endangered		0
Triphora gentianoides (Sw.) Nutt. ex Ames & Schltr.	G4; SNR					0
Triphora trianthophora (Sw.) Rydb.	G3; SH, S1-S3, SNR			Endangered	Endangered	0
Triphora yucatanensis Ames	G1; S1					0
Tropidia polystachya (Sw.) Ames	G4; S1			Endangered		1
Vanilla barbellata Rchb. f.	G4; S2			Endangered		7
Vanilla dilloniana Correll	G3; SNR			Endangered		5
Vanilla inodora Schiede						1
Vanilla mexicana Mill.	G3; S1			Endangered		2
Vanilla phaeantha Rchb. f.	G4; S1			Endangered		8

* Listed in original publication under a synonymous name.

[a] Conservation assessments by NatureServe correspond to Global threats: G1 = Critically Imperiled, G2 = Imperiled, G3 = Vulnerable, G4 = Apparently Secure, G5 = Secure, GU = Unrankable, GNR = Not Yet Ranked, GNA = Not Applicable. Subnational threats follow similar values (S1 to S5, etc.), but apply at the state or provincial levels. NatureServe rankings are available through <http://www.natureserve.org/explorer>.

[b] International Union for Conservation of Nature and Natural Resources (IUCN), 2011.

[c] Endangered Species Act (ESA), 1973; U.S. Government Printing Office, 2012.

[d] U.S. State listing is at the highest level of protection among all states listed, as reported by the USDA PLANTS Database (USDA, NRCS, 2012).

[e] Species at Risk Act (SARA), 2002.

[f] The number of botanic gardens where the orchid species is conserved or present, according to Botanical Gardens Conservation International (2012).

Table 2. Species distribution among listed orchid genera in Table 1.

Genus	Species #	Percent of total species
Platanthera Rich.	35	16.7%
Spiranthes Rich.	23	11.0%
Cypripedium L.	12	5.7%
Piperia Rydb.	10	4.8%
Malaxis Sol. ex Sw.	9	4.3%
Epidendrum L.	8	3.8%
Corallorhiza Gagnebin	7	3.3%
Neottia Guett.	7	3.3%
Calopogon R. Br.	5	2.4%
Hexalectris Raf.	5	2.4%
Triphora Nutt.	5	2.4%
Vanilla Mill.	5	2.4%
Goodyera R. Br.	4	1.9%
Habenaria Willd.	4	1.9%
Liparis Rich.	4	1.9%
Cleistesiopsis Pansarin & F. Barros	3	1.4%
Prosthechea Knowles & Westc.	3	1.4%
Bletia Ruiz & Pav.	2	1%
Cyclopogon C. Presl	2	1%
Dactylorhiza Neck. ex Nevski	2	1%
Dendrophylax Rchb. f.	2	1%
Dichromanthus Garay	2	1%
Eulophia R. Br. ex Lindl.	2	1%
Galeandra Lindl.	2	1%
Isotria Raf.	2	1%
Platythelys Garay	2	1%
Ponthieva R. Br.	2	1%
Sacoila Raf.	2	1%
Schiedeella Schltr.	2	1%
Anoectochilus Blume	1	0.5%
Aplectrum Blume	1	0.5%
Arethusa L.	1	0.5%
Basiphyllaea Schltr.	1	0.5%
Beloglottis Schltr.	1	0.5%
Brassia R. Br.	1	0.5%
Bulbophyllum Thouars	1	0.5%
Calypso Salisb.	1	0.5%
Camaridium Lindl.	1	0.5%
Campylocentrum Benth.	1	0.5%
Cephalanthera Rich.	1	0.5%
Cranichis Sw.	1	0.5%
Cyrtopodium R. Br.	1	0.5%
Eltroplectris Raf.	1	0.5%
Encyclia Hook.	1	0.5%
Epipactis Zinn	1	0.5%
Galearis Raf.	1	0.5%
Govenia Lindl.	1	0.5%
Hammarbya Kuntze	1	0.5%
Heterotaxis Lindl.	1	0.5%
Ionopsis Kunth	1	0.5%
Lepanthopsis Ames	1	0.5%
Macradenia R. Br.	1	0.5%
Mesadenus Schltr.	1	0.5%
Microthelys Garay	1	0.5%
Oncidium Sw.	1	0.5%
Pelexia Poit. ex Lindl.	1	0.5%
Peristylus Blume	1	0.5%
Pogonia Juss.	1	0.5%
Polystachya Hook.	1	0.5%
Prescottia Lindl.	1	0.5%
Pseudorchis Ség.	1	0.5%
Stelis Sw.	1	0.5%
Tipularia Nutt.	1	0.5%
Tolumnia Raf.	1	0.5%
Trichocentrum Poepp. & Endl.	1	0.5%
Tropidia Lindl.	1	0.5%

Table 2. Continued.

state and provincial species numbers are according to the NatureServe Explorer (NatureServe, 2011). Three species are endemic to California, as *Piperia colemanii* Rand. Morgan & Glic., *P. yadonii* Rand. Morgan & Ackerman, and *Platanthera yosemitensis*, and three to Hawaii, as *Anoectochilus sandvicensis* Lindl., *Liparis hawaiensis* H. Mann, and *Peristylus holochila* (Hillebr.) N. Hallé. Two orchid species are endemic to Florida, *Govenia floridana* P. M. Br. and *Triphora craigheadii* Luer; one species is endemic, each to three states, with *Spiranthes delitescens* Sheviak in Arizona, *S. infernalis* Sheviak in Nevada, and *S. parksii* Correll in Texas.

TARGET 2, AN ASSESSMENT OF THE CONSERVATION STATUS OF ALL KNOWN PLANT SPECIES, AS FAR AS POSSIBLE, TO GUIDE CONSERVATION ACTION

Only two North American orchids have been assessed by the International Union for Conservation of Nature and Natural Resources (IUCN) and are listed as threatened on the 2011 IUCN Red List of Threatened Species (IUCN, 2011): *Anoectochilus sandvicensis* as Vulnerable (or VU), and *Platanthera praeclara* Sheviak & M. L. Bowles, as Endangered (or EN).

The U.S. Endangered Species Act (ESA; 1973; U.S. Government Printing Office, 2012) federally lists the four endangered species *Piperia yadonii*, *Peristylus holochila* [≡ *Platanthera holochila* (Hillebr.) Kraenzl.], *Spiranthes delitescens*, and *S. parksii*, as well as the four threatened species as *Isotria medeoloides*, *Platanthera leucophaea* (Nutt.) Lindl., *P. praeclara*, and *S. diluvialis* Sheviak, and the one candidate species, *Platanthera integrilabia* (Correll) Luer. At the state level, 57% (119 species) are protected as endangered, threatened, vulnerable, or sensitive in at least one state (cf. Table 1).

The Canadian Species at Risk Act (SARA; 2002) lists seven endangered orchid species, as *Cypripedi-*

um candidum Muhl. ex Willd., *Isotria medeoloides*, *I. verticillata* (Muhl. ex Willd.) Raf., *Liparis liliifolia* (L.) Rich. ex Lindl., *Platanthera leucophaea*, *P. praeclara*, and *Triphora trianthophora* (Sw.) Rydb. Further, one threatened species, *Cephalanthera austiniae* (A. Gray) A. Heller, is included, as well as one species that is noted of special concern for conservation, *Epipactis gigantea* Douglas ex Hook. (cf. Table 1).

All but 10 species of the 210 orchid names included in Table 1 have been assessed by NatureServe (2011), with 24% (50 species) listed as globally threatened. Of these 50 threatened species, 11 were assessed at the global scale as critically imperiled (G1), 13 are imperiled (G2), and 26 are vulnerable (G3; cf. Table 1). For subnational assessments by NatureServe, 14% (30 species) are presumed to be extirpated from at least one state or province, and an overlapping 23% (48 species) are possibly extirpated from at least one state or province. Also at the subnational level, 84% (176 species) are variably threatened (ranging from S1 or critically imperiled, S2 or imperiled, or S3 or vulnerable) in at least one state or province. In all cases, where an orchid had been extirpated in one or more states, it was also threatened or endangered in at least one other state.

TARGET 3, INFORMATION, RESEARCH AND ASSOCIATED OUTPUTS, AND METHODS NECESSARY TO IMPLEMENT THE STRATEGY DEVELOPED AND SHARED

As indicated by Stewart (2008), much of the information on conservation and reintroduction of orchids has been published in the "gray" literature and obtained from unreplicated efforts that are rarely designed as scientific studies to obtain statistically significant data. Academic research occasionally addresses aspects of orchid biology, but rarely includes the whole process from basic biology to application for conservation or reintroduction (e.g., Kindlmann et al., 2002; Dixon et al., 2003). Replicated assessment of conservation is sorely lacking. There are three major areas of orchid biology that urgently need additional research: (1) identification of fungi associated with nearly all orchids, (2) understanding of how those fungi contribute to seed germination in situ and in vitro, and (3) how to maximize survival of cultured seedlings or plants.

Seed banking alone cannot successfully preserve orchids, because using the seeds to eventually cultivate and restore plants in nature requires that appropriate mycorrhizal fungi are present, especially at the orchid's protocorm stage. Identifying, maintaining, and establishing the symbiotic fungi needed for orchid seed germination is technically difficult and requires specialized equipment (Liu et al., 2010; Seaton et al., 2010; Stewart & Hicks, 2010). However problematic, this is essential for propagation and establishment of self-sustaining populations. Few organizations have the capacity to handle these unique aspects of orchid biology, placing cultivation and reintroduction beyond the abilities of nearly all conservation agencies. Scientific research has made substantial progress in overcoming these difficult aspects of orchid ecology, but additional efforts are needed on all key elements of orchid life histories that must be understood if we are to successfully support conservation, reintroduction, and propagation efforts for native orchids. The techniques being developed by scientists are still, and likely will remain, beyond the capacity of most conservation agencies, and there exists no current network for scientific researchers either to support conservation program managers or to communicate with commercial or private growers and garden enthusiasts who would benefit from a more complete understanding of all aspects of orchid growth, cultivation, and conservation.

TARGET 7, AT LEAST 75% OF KNOWN THREATENED PLANT SPECIES CONSERVED IN SITU

When considering the proportion of threatened orchids that are conserved in situ, it is important to distinguish between species that are considered globally threatened and the majority of orchids that are threatened within a portion of their ranges. Conserved in situ means "that biologically viable populations of these species occur in at least one protected area or the species is effectively managed outside the protected area network, e.g., as part of a management plan" according to a recent GSPC Plant Conservation Report (Convention on Biological Diversity [CBD], 2009: 23–24). As previously outlined (cf. Table 1), of the 50 globally threatened (i.e., ranked G1, G2, or G3 by NatureServe) orchid species, only eight are protected under the ESA and one additional species, *Triphora trianthophora*, under Canada's SARA. An additional 22 species are protected at the state or province level. Taken together, a total of 62% (31 of 50 species, cf. Table 1) of native orchid species assessed as threatened are thus conserved in situ (i.e., have legal protection), which is far below the goal of Target 7. It is noteworthy that six of the 10 globally imperiled or critically imperiled species (G1 or G2) that currently have no protection at the federal or state level have only recently been described, suggesting that accurate identification and species delimitation have hampered attempts at species protection.

Beyond recognition of the need to protect orchid taxa is the degree to which protection is actually accomplished. The level of protection provided by state or federal protected status depends on both the number and distribution of plants on protected land and also on the knowledge of the species' biology needed to determine whether protection is adequate. A number of protected reserves in the United States and Canada focus to some degree on orchids or on habitats with disproportionately many orchids. One such example is the Bruce Peninsula National Park in Ontario, which supports 43 of the orchid species native to Canada that will be threatened as a result of climate change (Suffling & Scott, 2002). The heart of the Niagara Escarpment Biosphere Reserve includes the Bruce Peninsula National Park, a Nature Conservancy Preserve, and First Nations lands, all of which share knowledge about species at risk. The stated park goal is to maintain viable populations of all native species in situ, and there is a program underway to report on the condition of all SARA species, including trends in populations and the factors that contribute to their condition.

Attributing population trends to particular factors highlights the importance of in-depth understanding of species biology for accomplishing effective conservation. Most endangered orchids in North America have had at least some investigation of population genetic structure, and this has been used to understand connectivity between populations and to determine the contribution of outlying populations to species integrity. For example, Wallace (2003) found that *Platanthera leucophaea* was a predominantly outcrossing species and that inbreeding depression, especially in small populations, suppressed seed viability. These results suggested that larger, more diverse and outcrossing populations were needed to support population genetic variability in the current fragmented landscape. This white-fringed orchid historically was distributed from Missouri and Iowa to Ontario with disjunct populations in Maine, New Jersey, and Virginia (Bowles et al., 2005). The current distribution is, however, much reduced and few populations are self-sustaining.

Also important to consider are critical issues of land management. Many terrestrial orchids are pioneer species and cannot compete with overgrown habitat. One prime example is the Green Swamp Preserve of southeastern North Carolina in Brunswick and Columbus counties. Originally established to protect the habitat of the Venus fly trap (*Dionaea muscipula* J. Ellis, Droseraceae), a great variety of orchids, including species of *Calopogon* R. Br., *Platanthera*, and *Cleistes* Rich. ex Lindl., exist in the preserve. The reserve's 17,424 acres are owned and managed by The Nature Conservancy, and its longleaf pine savannas must be periodically subjected to prescribed burns to keep the habitat prime for the smaller, herbaceous species that would be otherwise crowded out by succession.

In contrast, other woodland species, such as *Cypripedium acaule* Aiton, *C. fasciculatum* Kellogg ex S. Watson, *C. montanum* Douglas ex Lindl., and *C. reginae* Walter, have ecological strategies and dependencies based both on edaphic constancy and occasional disturbance of their environments. For example, even though *C. fasciculatum* and *C. montanum* grow sympatrically in old growth forest, there is evidence that *C. montanum* needs occasional disturbances, such as fire or tree-felling and thinning, to create open, sunnier areas in which they will bloom and set seed more freely. Its sympatric relative, *C. fasciculatum*, conversely seems to be inhibited by burns and other such disturbances. Therefore, it becomes increasingly important to investigate the individual ecological complexities of each individual species if comprehensive management plans are to be created.

Understanding what factors influence population dynamics is critical for understanding how species will respond to warming global temperatures. With orchids, this uncertainty may be compounded by considering the other species on which they depend. Some orchids may be limited by the availability of pollinators. For example, the deceptive orchid *Cyrtopodium punctatum* (L.) Lindl. depends on oil-gathering *Centris* bees for pollination. These bees rely on other flowering plants, especially *Byrsonima lucida* (Sw.) DC. (Malpighiaceae), for the oils they collect. This led Pemberton and Liu (2008) to suggest that *B. lucida*, which is almost completely absent from the areas where the few remaining native orchid populations of *C. punctatum* persist, be planted in the vicinity of orchids to attract and support the bees that pollinate both taxa. Such activities may also be needed to support the interaction between orchids and their pollinators in the face of climate change. In particular, Liu et al. (2010) suggested that warming temperatures in southwestern China are differentially affecting pollinator and orchid phenologies such that availability of pollinators and orchid flowering may be increasingly out of synchronization. Effects of climate change on orchid mycorrhizal fungi are completely unknown, reflecting that very little is known about what factors drive the distribution and abundance of nearly all fungi. Because of this, conservation of fungi must be largely accomplished through habitat conservation.

TARGET 8, AT LEAST 75% OF THREATENED PLANT SPECIES IN EX SITU COLLECTIONS, PREFERABLY IN THE COUNTRY OF ORIGIN, AND AT LEAST 20% AVAILABLE FOR RECOVERY AND RESTORATION PROGRAMS

The Botanical Gardens Conservation International's (BGCI; 2012) Plant Search database shows that 66% (139 species) of native North American orchids are found in ex situ collections in botanical institutions around the world (Table 1). Each of these species is reported from an average of six botanic gardens, but more than 25% (36 species) are reported from a single botanic garden only. The species most prevalent is *Prosthechea cochleata* (L.) W. E. Higgins [≡ *Encyclia cochleata* (L.) Dressler], a species easily propagated (Pugh-Jones, 2009), which is reported from 65 botanic gardens. Only two of 11 species ranked G1 by NatureServe are found in any botanic garden collection, being *Peristylus holochila* at three gardens and *Spiranthes delitescens* at one institution. Five of 13 species ranked G2 are represented in botanic gardens, but only two are reported from more than one garden (two and five gardens, *Platanthera leucophaea* and *S. diluvialis*, respectively). It is highly unlikely that any of these ex situ collections represents a genetically representative sample of the species.

The major method likely to preserve species genetic variation is seed banking, as storing many genetically distinct orchid seeds requires very little space. Accomplishing such genetically representative conservation is a major goal of the project Orchid Seed Stores for Sustainable Use (OSSSU; Seaton et al., 2010). This project is initially focusing on hotspots of orchid diversity but is also beginning to work with groups within North America to organize locations and organizations for genetically representative orchid seed storage. The Center for Plant Conservation (CPC; <http://www.centerforplantconservation.org>) maintains seed collections for eight orchid species, two of which are ranked G1 (*Peristylus holochila* and *Spiranthes delitescens*), three G2 (*Isotria medeoloides*, *Platanthera leucophaea*, and *S. diluvialis*), and three G3 (*Cypripedium kentuckiense* C. F. Reed, *Platanthera praeclara*, and *S. parksii*). These species are specifically directed to be available for conservation and restoration activities, so this would suggest that seeds of 16% (eight of 50) of threatened North American orchid species are available for conservation and restoration, though the extent to which their collections are genetically representative is unclear.

One shortcoming of seed storage for orchids is that all orchids are dependent on or benefit from mycorrhizal fungi for seed germination and all species are dependent on fungi for protocorm growth. While fungal requirements can sometimes be overcome under specialized conditions in the laboratory, there is little question that under natural conditions fungi are required for orchid recruitment and long-term survival of populations. Many orchids require specific fungi at all life history stages (e.g., McCormick et al., 2004), while other more generalist orchids use fungi from one or a few families (e.g., Shefferson et al., 2010). As a result, effective ex situ conservation of orchids will require not just seed banking, but also maintenance of required mycorrhizal fungi. This goal is still far from being accomplished. One of the central difficulties has been to simply identify the needed fungi. Most orchid mycorrhizal fungi rarely produce spores and so were known only from the anamorphic stage for many years. Now they can be identified largely by DNA sequencing. This rarity of spore production, coupled with inconspicuous and morphologically depauperate sporulating bodies, has resulted in a poorly defined taxonomy of these cryptic fungi (e.g., Swarts & Dixon, 2009); DNA sequences rarely match the taxonomically described species. Furthermore, with few spores produced, the fungi that an orchid needs can rarely be stored as spores and so must be maintained as active cultures. However, some researchers have been testing methods for storing fungal cultures in liquid nitrogen (Batty et al., 2001). If these methods prove successful, then conservation of genetically representative collections of mycorrhizal fungi may become more common.

As yet there are relatively few orchid mycorrhizal fungi in culture. The University of Alberta Mycological Herbarium's (UAMH; <http://www.uamh.devonian.ualberta.ca>) culture collection currently maintains 113 fungal cultures obtained from 37 orchid species. The Smithsonian Environmental Research Center (SERC) currently maintains more than 400 fungal isolates in culture from more than 40 native orchid species (D. F. Whigham, M. K. McCormick & J. P. O'Neill, pers. comm.). The American Type Culture Collection (ATCC) maintains 30 isolates from 13 orchid species (<http://www.atcc.org>). Other scattered fungal cultures exist in laboratories around the country where orchid research is conducted, but the maintenance of these collections is often uncertain. Most of the existing collections focus on saprotrophic *Tulasnella* J. Schröt. and *Ceratobasidium* D. P. Rogers fungi, while many orchids rely on fungi that form ectomycorrhizal associations with other plants. These fungi are often difficult to culture and many cannot be grown without a photosynthetic host, often a tree, making them very

difficult to establish or maintain in culture. Even when fungi are available in culture, however, their role in facilitating seed germination is far from certain.

Germination requirements for seven of 11 G1-ranked and five of 13 G2-ranked orchids have yet to be studied (Stewart & Hicks, 2010). One threatened orchid (*Isotria medeoloides*) has so far proven completely recalcitrant in culture or in the field. Of the 11 G1- and G2-ranked orchids for which some level of germination success has been obtained, two have had only limited asymbiotic success and only five have been germinated symbiotically. Symbiotic germination has not been reported for the other six of these 11 species. Symbiotic germination is expected to be the method that leads to seedlings best able to survive reintroduction and also provides a method for co-introducing needed fungi and orchids (e.g., Stewart, 2008).

Few well-documented orchid reintroductions exist. Often reintroductions occur in one location at one time and either succeed or fail without providing information about what may have been suboptimal or may increase success in the future (Stewart, 2008). Two examples of reintroductions designed as studies are outlined by Stewart (2008). Elements of another reintroduction are described by Zettler and Piskin (2011). All three studies were designed to assess effectiveness of introduction into different habitats, but only one utilized symbiotic seedlings because fungi were not available for the other two species. In two of the three studies, survival was highest in sites that already had the target orchid species. In the third study, reintroduction was only attempted in sites with the target species so existing plants could act as sources for mycorrhizal colonization of the transplants. This suggests that mycorrhizal colonization may be critical for reintroduction success. No mention of pollinator availability was made in these three studies.

TARGET 11, NO SPECIES OF WILD FLORA ENDANGERED BY INTERNATIONAL TRADE

The United States and Canada are both parties to The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; <http://www.cites.org>), the lead coordinating agency for the implementation, monitoring, and review of Target 11. All orchid species are listed in CITES appendix II, thus preventing the endangerment of North American orchids by over-exploitation caused by international trade. Artificially propagated plants, hybrids, plant parts, products, or derivatives, with a few exceptions, require permits or certificates to import, export, or re-export orchid species across international lines. However, the smuggling of wild orchids remains a problem (Phelps et al., 2010).

TARGET 14, THE IMPORTANCE OF PLANT DIVERSITY AND THE NEED FOR ITS CONSERVATION INCORPORATED INTO COMMUNICATION, EDUCATION, AND PUBLIC AWARENESS PROGRAM

As environmental awareness matures and enters the digital age, several organizations previously limited to spreading their messages slowly though periodicals and mailings have found much broader and enthusiastic younger audiences. One example is the Native Orchid Conference (<http://tech.groups.yahoo.com/group/nativeorchidconference/>) that has become the "go to" place for information about native orchid species and access to experts, photographs, ecology, phenology, and field information to any interested party. It is particularly useful to the public, who may not otherwise have access to or might be intimidated by scientific publications.

Botanical institutions nationwide, such as the Smithsonian Institution and the U.S. Botanic Garden (USBG), provide a type of outreach through conservation messages that regularly appear in exhibits, particularly annual orchid exhibits, and are viewed by their many visitors. In addition, speakers from these institutions regularly travel around the country discussing conservation values to likely interested parties at orchid societies and special events across North America. These efforts, however, are not sufficient. Considerably more could, and should, be done to raise public awareness about the importance of North American native orchid species.

TARGET 15, THE NUMBER OF TRAINED PEOPLE WORKING WITH APPROPRIATE FACILITIES SUFFICIENT ACCORDING TO NATIONAL NEEDS, TO ACHIEVE THE TARGETS OF THIS STRATEGY

Without a centralized organization focusing on North American orchids, it is difficult to assess how many trained individuals work on the in situ and ex situ conservation of orchid species. Kramer et al. (2010) report on a U.S. survey that revealed a major decline in botanical courses and degree programs at universities and colleges nationwide, as well as a deficiency of botanists at U.S. government agencies. With fewer college graduates entering the botanical workforce and many government botanists retiring in the coming years, it will be difficult to increase the number of trained people working on orchid taxonomy and conservation.

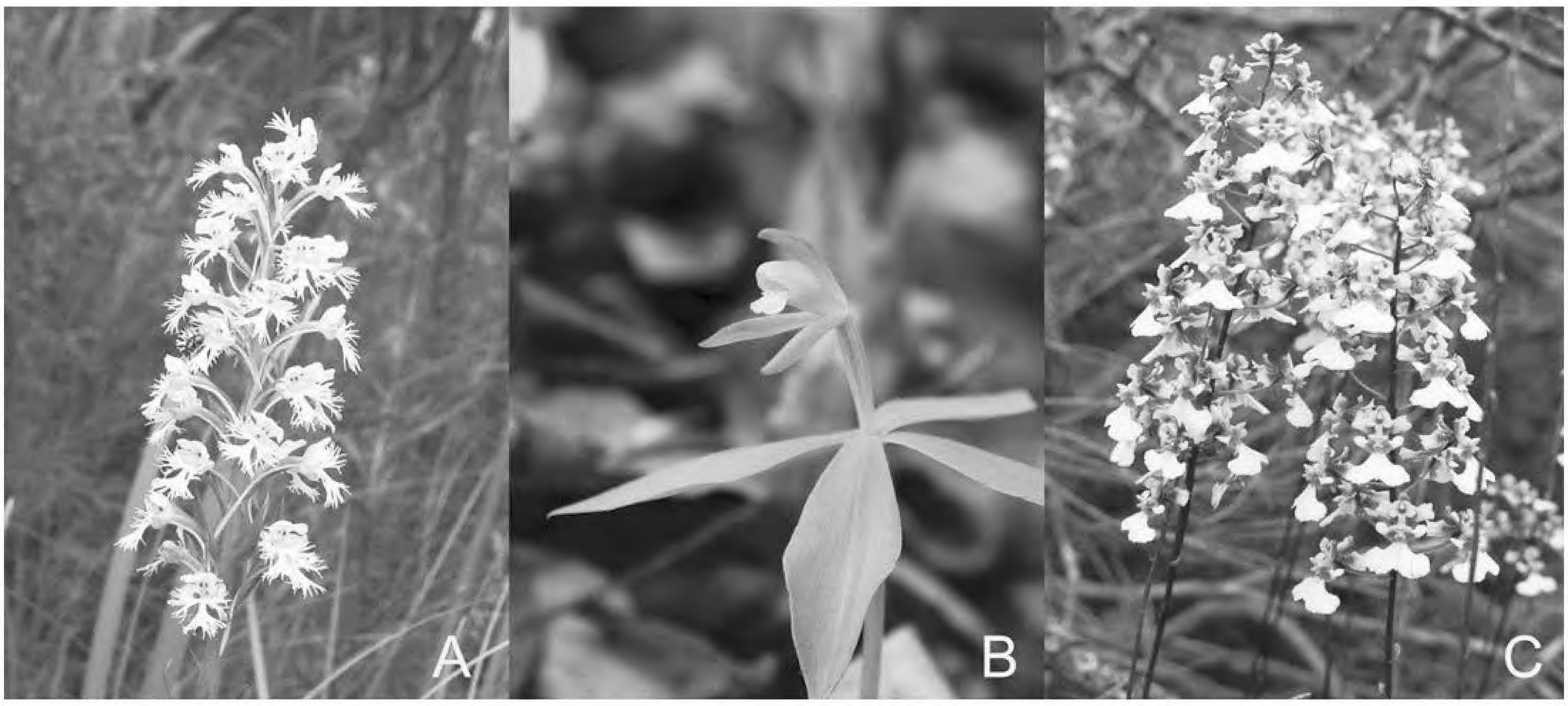


Figure 1. Three endangered orchid species. —A. *Platanthera leucophaea* (Nutt.) Lindl. (photo by Timothy Bell). —B. *Isotria medeoloides* (Pursh) Raf. (photo by Melissa McCormick). —C. *Tolumnia bahamensis* (Nash) Braem. (photo by Matt Richards).

TARGET 16, INSTITUTIONS, NETWORKS, AND PARTNERSHIPS FOR PLANT CONSERVATION ESTABLISHED OR STRENGTHENED AT NATIONAL, REGIONAL, AND INTERNATIONAL LEVELS TO ACHIEVE THE TARGETS OF THIS STRATEGY

The CPC is a successful network of botanic institutions dedicated to preventing the extinction of U.S. native plants by ensuring that ex situ material is available for restoration and recovery efforts. Orchids, however, are unique in that effective ex situ conservation of orchids requires not just seed banking, but also maintenance of cultures of required mycorrhizal fungi. A network of partnerships focusing exclusively on the needs of orchids is necessary.

Three Case Studies

As described throughout this manuscript, effective conservation of any orchid species is a complex undertaking that includes a wide range of variables from long-term storage and maintenance of collections of materials (e.g., seeds and mycorrhizal fungi) that would be required for cultivation and propagation to the establishment and maintenance of habitats that support the long-term success of orchid populations. For many of the reasons described above, we are unaware of any effort that has been fully successful in assuring the long-term survival of any native orchid species. There are, however, a few examples of the efforts that are necessary to build an information base, which can support further attempts to conserve all native orchid species.

Effective orchid conservation must integrate the understanding of existing and future environmental threats, taxonomic distinctiveness, numbers of individuals in populations, reproductive biology, ex situ propagation, and the maintenance of evolutionary processes influencing population distribution patterns. In order to do this, conservation must combine detailed experimentation directed at continued survival of the species both in situ and ex situ (Ramsay & Dixon, 2003). The integrated conservation strategy emphasizes the study of interactions among land conservation, biological management, research and propagation and reintroduction and habitat restoration (Hopper, 1997).

CASE 1

Platanthera leucophaea (Fig. 1A) is currently listed as federally threatened, under the ESA, and has declined in the United States by more than 70% from estimates provided by original county records. This decline has mainly been due to habitat loss. Most of the remaining 79 populations are small, these with fewer than 50 plants, and only 28% have adequate protection and management (U.S. Fish and Wildlife Service, 2007). Investigation of the orchid's genetics indicates that the species is primarily outcrossing and demonstrates significant inbreeding depression particularly prevalent in small populations (Wallace, 2003). Despite the low number of protected populations, the outlook for conservation of *P. leucophaea* is relatively good. Well-coordinated efforts to recover this species are currently in place and involve a network of scientists, private landowners, and volunteers (Zettler & Piskin, 2011). Fungi needed by *P. leucophaea* are known, and symbiotic germination is regularly accomplished in laboratory cultures, although successful transplantation of seedlings into natural populations has met with

limited success (Zettler et al., 2005; Zettler & Piskin, 2011). Genetic surveys have found that even small populations of *P. leucophaea* may retain relatively high levels of genetic diversity (Holsinger & Wallace, 2004), potentially resulting in significant seed production and recruitment where habitat is available. This level of information about the species and the network of public and private agencies cooperating toward the orchid's conservation suggest that *P. leucophaea* has a strong potential for recovery.

CASE 2

In contrast to the favorable outlook for *Platanthera leucophaea*, *Isotria medeoloides* (Fig. 1B) is listed by NatureServe as imperiled (G2) in 14 (78%) of the 18 states and provinces in which it is still known to occur; the orchid is thought to be historical or extirpated in five states. Nowhere across its distributional range in eastern North America is *I. medeoloides* considered secure or common. The primary threat to its existence is destruction of its woodland habitat for development or forestry. The majority of its populations number fewer than 25 plants and are thus vulnerable to local extinction (U.S. Fish and Wildlife Service, 1994). Many of the extant populations, including some of the largest populations, occur on land protected by federal or state agencies or the U.S. military, and on this basis the plant might be considered well protected (U.S. Fish and Wildlife Service, 1994). Its preferred habitat conditions have also been identified (Sperduto & Congalton, 1996), and searching these habitat types allowed researchers to locate many new populations in the late 1990s. However, the plant's biology throughout much of its range is defined by many small, ephemeral populations that make it quite difficult to target areas to protect. Additionally, long periods of dormancy, common in many terrestrial orchids, are characteristic of the lifecycle of this species, making it difficult to assess population sizes or even plant presence (Mehrhoff, 1989).

Ongoing management experiments of *Isotria medeoloides* are beginning to reveal a management technique, tree thinning, which can benefit local populations (e.g., Brumback et al., 2011). The fungi needed by this orchid have recently been identified (M. K. McCormick, unpubl. data), but they have so far been resistant to culture in the laboratory. Seed germination, either symbiotic or asymbiotic, has never been accomplished either in the field or in the laboratory, yet based on population demographic studies (Mehrhoff, 1989) and preliminary genetic analyses (M. K. McCormick, unpubl. data), recruitment from seed is critically important to both population persistence and also the founding of new populations. This suggests that this species, many of whose extant populations are relatively well protected, is sufficiently poorly understood and that its maintenance in the face of a changing climate is a serious concern.

CASE 3

An additional case study involved returning a semiepiphytic species, *Tolumnia bahamensis* (Nash ex Britton & Millsp.) Braem (Fig. 1C), to reasonably pristine habitat, where ostensibly all the other pieces of the ecological puzzle remain. In this case, suitable unspoiled, historical habitat in Jonathan Dickinson State Park in southern Florida was assessed and the few extant plants of *T. bahamensis* were cross-pollinated and grown ex situ at Atlanta Botanical Garden. With most of the host plants and presumably mycorrhizal fungi intact in the orchid's preferred environment, reintroduction has initially been successful. These types of enrichment reintroductions should be attempted whenever suitable protected habitat is available. This underscores the need for a holistic approach to orchid conservation in which entire habitats and ecosystems are sought to be preserved whenever possible (Jonathan Dickinson State Park, 2011).

The Future of Orchid Conservation

International efforts such as CITES have focused on the illegal trade of orchids and many organizations have been established to cultivate, market, and enjoy orchids, but there is no one national organization that focuses on their conservation and restoration. Neither is there one entity devoted to educating the public about the evolutionary and ecological importance of orchids. Organizations (e.g., federal agencies and the U.S. military) that are mandated to identify and protect orchids on public lands have been involved in research on relatively few species (see examples above), and they rely mostly on habitat conservation for management. While habitat management is important, ecological attributes of orchids (e.g., the obligatory relationships between orchids and fungi at critical life history stages) dictate that habitat management alone will not result in orchid conservation or restoration. Every U.S. state lists at least one orchid species that is rare or threatened and most states list multiple orchid species. There is, however, little coordination among states and no one organization that can provide answers to basic questions that would guide effective management plans. Private land-management conservation groups (e.g., The

Nature Conservancy) face a similar dilemma. Perhaps most important, the public has little recognition of the diversity and importance of orchids and there is no central organization that focuses on orchids as an important aspect of education and outreach to the public.

We propose a possible solution to the lack of coordination and the pooling of resources to focus on the more than 200 native orchids listed within the United States and Canada. The NAOCC (http://northamericanorchidcenter.org) is the first internationally focused public–private effort to support the conservation, cultivation, and restoration of native orchid species. NAOCC began as a collaborative effort between the SERC, Smithsonian Gardens, Department of Botany at the National Museum of Natural History (NMNH), Exhibits and Park Management Department of the National Zoological Park (NZP), and USBG. Other government agencies, botanic gardens, and public and private landowners are joining the collaboration. NAOCC launched in 2012 and the network that will support the effort will be developed over approximately 10 years.

The NAOCC's mission is to conserve the native orchid heritage of the United States and Canada through preservation, restoration, and cultivation of native orchids and to convey the importance of NAOCC to the public through innovative educational programs. The goals of NAOCC are to:

- Develop an international seed bank collection, in collaboration with the CPC, that will be representative of the genetic diversity of all North American orchid species.
- Develop an international collection of fungi representative of the genetic diversity of mycorrhizal fungi required by native orchids.
- Develop techniques to conserve the genetic diversity of all native orchids by cultivating them in an international network of botanic gardens and arboretums.
- Use seed and mycorrhizal fungal banks to develop techniques for restoring, conserving, cultivating, and restoring orchids in native habitats.
- Support efforts to conserve orchid populations through habitat conservation and restoration.
- Develop web-based materials that will provide up-to-date information on the ecology, conservation status, and techniques for the cultivation of North American orchids.

An initial goal of the network of botanic gardens is to grow and display all native orchids in the United States and Canada using an ecoregional approach. The primary partners play different yet integrated roles. NAOCC administration and research are based at the SERC, which provides research services to private and public organizations, and collaborates with the CPC and other affiliated organizations (e.g., Kew Gardens and the U.S. Bureau of Land Management's Seeds of Success program) to develop a genetically diverse seed bank for all native orchids. The seed collection will not only be used to assure the long-term survival of the germplasm of each species, but will also serve as a resource for material to support efforts to grow and cultivate all native orchids. SERC is collaborating with the partners of NAOCC to expand its collection of orchid mycorrhizal fungi to include fungi from all native orchids. SERC is also playing a lead role in developing a network of laboratories that provides services for the molecular analysis of orchid fungi. The Smithsonian's Department of Botany at the NMNH will focus on the development of a well-curated and complete herbarium-based orchid collection and will develop DNA barcodes for all North American orchids. NMNH will also develop a digital library of all North American orchids, including visual images of all species, and will actively partner with SERC and NAOCC to develop web-based technologies to provide up-to-date public access to orchid information. Smithsonian Gardens, the Exhibits and Park Management Department of the NZP, and the USBG will coordinate efforts to cultivate all orchids within the Washington ecoregion into their living collections, and they will collaborate with partner-gardens to develop and put into effect a plan to cultivate all 210 native orchids in a range of gardens across the United States and Canada. The Smithsonian and the USBG will also include exhibits about native orchids in their biannual orchid show.

Conclusion

Native orchids occur in every state in the United States and every Canadian province, and one or more species is listed as endangered or threatened in every state and province. As described above, national and international efforts have provided a degree of protection for native orchids, and there have been efforts to conserve and restore a small number of species. It is our view that progress toward the effective conservation of the numerous species that are listed as threatened or endangered will require a large-scale integrated effort to develop the knowledge base required to develop effective management strategies to assure the survival of the more than 200 species of native orchids. In establishing the NAOCC, our goal is to develop the resource base and integration of public and private organizations

responsible for or interested in native orchids to ultimately assure the survival of all native orchid species. The success of NAOCC will require long-term commitments to obtain the financial support for the research, training, and education necessary to reach the organization's goal of conserving the genetic diversity of all native orchid species.

In addition to botanic gardens, research organizations, and private and public groups devoted to orchid conservation, the success of NAOCC will also require the establishment of a dynamic web site and associated web-based materials that will enlist the public in the effort. The ultimate success of NAOCC and its partner organizations is important for other reasons. While the orchid family is the most diverse family of flowering plants on earth, the number of species in the United States and Canada is relatively small, and conserving our native orchids would be a success that has never been obtained. Orchids are more than just beautiful flowers. They are an important component of North America's ecology, biological richness, and heritage, and they need greater protections than they currently receive. With so many uncertainties in the future due to habitat degradation, urban sprawl, and climate change, it is incumbent on organizations with the infrastructure necessary to guide and coordinate the efforts of the many individuals and organizations that have a stake in native orchid preservation. NAOCC seeks to be this important resource for North American orchid species and ultimately to serve as a model for similar conservation organizations in other parts of the world.

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TOWARD TARGET 2 OF THE GLOBAL STRATEGY FOR PLANT CONSERVATION: AN EXPERT ANALYSIS OF THE PUERTO RICAN FLORA TO VALIDATE NEW STREAMLINED METHODS FOR ASSESSING CONSERVATION STATUS[1]

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ABSTRACT

Target 2 of the 2020 Global Strategy for Plant Conservation (GSPC) calls for a comprehensive list of the world's threatened plant species. The lack of such a list is one of the greatest impediments to protecting the full complement of the world's plant species, and work to achieve this has been slow. An efficient system for identifying those species that are at risk of extinction could help to achieve this goal in a timeframe sensitive to today's conservation needs. Two systems that efficiently use available data to assess conservation status were tested against a provisional International Union for Conservation of Nature and Natural Resources (IUCN) Red List analysis to evaluate the native seed plant species of Puerto Rico. It was demonstrated that both systems efficiently identify species at risk, which is a step toward both the GSPC Target 2 and a more comprehensive IUCN Red List for plants. Both systems were effective at identifying plant species at risk, with the New York analysis identifying 98% and the Smithsonian analysis 85% of the plant species considered Threatened in the IUCN Red List. Both analyses to some extent overestimated those plants at risk, but the species identified are all range restricted and, thus, of some conservation interest.

Key words: Global Strategy for Plant Conservation (GSPC), IUCN Red List, Puerto Rico.

Estimates of the number of flowering plant species vary widely, from about 250,000 to more than 400,000 (Stebbins, 1974; Prance et al., 2000; Govaerts, 2001; Bramwell, 2002; Miller, 2011), many with restricted ranges (Joppa et al., 2010), and perhaps more than a quarter of all flowering plants still have not been described and named (Prance et al., 2000; Miller, 2011). Furthermore, many of these species are at risk of extinction in the near future as a consequence of deforestation and habitat destruction and perhaps 94,000 species are so endangered (Pitman & Jorgensen, 2002). There is perhaps no

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greater impediment to ensuring that these threatened species persist into the future than the lack of a comprehensive list of those plant species that are at risk and most desperately need our conservation attention.

The Global Strategy for Plant Conservation (GSPC) was adopted at The Hague, The Netherlands, at the sixth meeting of the Conference of the Parties to the Convention on Biological Diversity (CBD) in 2002, establishing 16 targets under five broad aims designed to prevent the loss of plant diversity and encourage its sustainable use to improve human livelihoods (CBD, 2002). Target 1 of the GSPC was the production of "a widely accessible working list of known plant species, as a step towards a complete world flora," and Target 2 was "a preliminary assessment of the conservation status of all known plant species, at national, regional, and international levels." The GSPC was originally designed with the intention that targets would be met by 2010, and while some progress was made on some of the targets, they were not fully accomplished, and in 2010 in Nagoya, Japan, a revised GSPC with 2020 targets was adopted (CBD, 2010). In the 2011–2020 GSPC, Target 1 was revised as "an online flora of all known plants," and the second target remained similar to the original target, being "an assessment of the conservation status of all known plant species, as far as possible, to guide conservation action" (CBD, 2011).

While the GSPC Target 2 calls for a comprehensive survey of the conservation status of all plant species, it does not identify any specific method for performing the assessments. A variety of methods are in wide use for assessing threat, including Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO's) system used to assess threat for both plants and animals in Mexico (SEMARNAT, 2002) and the system of NatureServe (<www.natureserve.org>), but the most widely used procedure has been that of the International Union for Conservation of Nature and Natural Resources (IUCN) Red List (IUCN, 2001, 2008, 2009, 2011), the only system that has been used to any significant degree globally. The Red List has been very successfully used to accomplish comprehensive assessments for amphibians (Stuart et al., 2008), birds (BirdLife International, 2008, 2013), and mammals (Schipper et al., 2008). However, collectively these vertebrate groups have fewer than 22,000 species, so completion of their conservation assessments is less daunting than it is for flowering plants, with more than 300,000 species, and to date less than 15,000 species of plants have been assessed (IUCN, 2011). Numerous Red Lists have been published, assessing the conservation status of species on a regional rather than global basis, but the only taxonomically comprehensive studies completed to date for plants are for cycads (Donaldson, 2003) and conifers (Farjon et al., 2006). The goal of the present study is to validate a streamlined system for rapid assessment of the conservation status of plant species that is complementary with the Red List procedures and to represent a first step toward accomplishing Red List analyses, but also with preliminary assessments that are useful for immediate conservation decisions.

Background

One benefit of the IUCN Red List system is its flexibility, allowing evaluation by any one of five different criteria, depending on the type of data available, thus making it applicable to a broad range of plant and animal groups (IUCN, 2001). The IUCN Red List methods identify Threatened species and assign them to categories of Vulnerable (VU), Endangered (EN), or Critically Endangered (CR), as threat increases. Demographic data gathered over time are seldom available for plants, but the geographic range of most plant species can be determined from locality data associated with herbarium specimens with a reasonable degree of accuracy, and used to calculate Extent of Occurrence (EOO) and Area of Occupancy (AOO; Willis et al., 2003; Brummitt et al., 2008). Under the IUCN Criterion B, species are considered Threatened if their EOO or AOO values fall below specified thresholds and if they also meet two of three additional subcriteria: (a) severe fragmentation or a small number of known localities, (b) continuing decline in range, habitat, number of subpopulations, or number of individuals, or (c) extreme fluctuation in range, habitat, number of subpopulations, or number of individuals (IUCN, 2001). While both EOO and AOO can be easily calculated from locality information from herbarium specimens, there are a number of confounding issues. All of the herbarium specimens of any given species are generally distributed throughout many of the world's herbaria, rather than being together in a single institution. Furthermore, locality data from only a tiny percentage of herbarium specimens have been entered into publically available databases and only a percentage of these records are associated with geographic coordinates required for geographic information system (GIS) analysis. Rigorous and comprehensive Red List analysis using the Red List's Criterion B thus requires assembly of a great amount of specimen locality data from multiple

herbaria and secondary efforts to georeference the records.

The less than 15,000 Red List assessments completed to date for plants are only a small step toward the GSPC 2020 Target 2, and a more efficient method than the Red List procedures could help generate the list of endangered plant species in a timeframe more sensitive to conservation needs. It seems preferable to use a streamlined procedure that would complement, rather than substitute for, the Red List system. Two systems have been developed with the aim of completing conservation assessments rapidly and efficiently, using readily available data (Miller et al., 2012), and they were tested by evaluating the global conservation status of Puerto Rican plant species and identifying those species that are At Risk. The terms "Not At Risk" and "At Risk" were specifically chosen as they do not overlap with IUCN's Red List category names and cannot be confused, but the At Risk category used here can be considered an approximation of IUCN's Threatened category, including the subcategories CR, EN, and VU. Both analyses used herbarium specimen locality data readily available in the Global Biodiversity Information Facility (GBIF) and institutional databases and did not require compilation of a set of data that was labor intensive to assemble. A detailed review of Puerto Rican native plants (Miller et al., 2012) produced provisional Red List assignments (pending their submission, approval, and acceptance by the Species Survival Program at IUCN), and results of the earlier studies were compared to validate the streamlined methods.

The flora of Puerto Rico was chosen as a test case for the proposed conservation assessment methods because it is a reasonable size, with 2009 native seed plant species (Acevedo-Rodríguez & Strong, 2007, 2008), it is comparatively well known for a tropical flora, and it is well documented by herbarium collections. Only 53 native plant species from Puerto Rico have been identified to date as globally Threatened in the Red List (IUCN, 2011; <www.iucnredlist.org>), but this number is almost certainly an underestimate as only a small percentage (3.9%; 76 species) have been evaluated. Therefore, the flora of Puerto Rico is in serious need of assessment. It is also an appropriate size to test the validity of two streamlined methods for the conservation assessment of plant species.

Methods

Geographic distribution information was compiled in a database hosted by The New York Botanical Garden (NY; The Puerto Rican Endangered Plants Initiative, 2012) to provide detailed information about the range of each seed plant species native to Puerto Rico. Herbarium specimen locality records from NY and GBIF from earlier analyses were supplemented with data from the Smithsonian Institution (US) and three Puerto Rican herbaria, the University of Puerto Rico, Río Piedras (UPRRP), the Jardín Botánico of the University of Puerto Rico (UPR), and the University of Puerto Rico, Mayagüez (MAPR). Two streamlined analyses were conducted to evaluate the global conservation status of Puerto Rican seed plant species. The New York Botanical Garden's GIS lab method (NYBG-GIS) calculated the EOO from the complete herbarium specimen locality database (Miller et al., 2012). EOO was calculated for all species with at least three unique known localities by creating a minimum convex polygon using the ArcGIS extension, Hawth's tools (Beyer, 2007), the smallest polygon that encompasses all specimen localities and has no angles that exceed 180° (IUCN, 2008). Areas of unsuitable habitat, such as large bodies of water, were excluded from the EOO calculations, using ArcGIS 9.2 (ESRI, 2007; IUCN, 2008). All species with EOO values greater than 20,000 km^2 were considered to be Not At Risk. For those with calculated EOO values below 20,000 km^2, collection data without geographic coordinates were retrospectively georeferenced, and EOO was recalculated. Those species with EOO values remaining below the 20,000 km^2 threshold were considered At Risk. The Smithsonian method (Krupnick et al., 2009), from the Plant Conservation Unit (US-PCU), is a four-step evaluation that considers temporal, spatial, and abundance data inferred from herbarium records from US. The species is considered At Risk if all known specimens were collected before 1900, if available collections are from five or fewer localities, or if the species is known from less than the median number of specimens per species collected since 1960 from the area being evaluated.

Species identified as At Risk in both analyses were considered to be of conservation concern, and those species that were identified as At Risk by one, but not both, analyses were subjected to further review. In August 2011, an expert panel was convened at the University of Puerto Rico's Botanical Garden to test the validity of the results of the streamlined analyses. The panel was comprised of botanists from the UPRRP, MAPR, the University Botanical Garden, NY, US, the USDA's Institute for Tropical Forestry, the Department of Natural and Environmental Resources, and the Fideicomiso de Conservación de Puerto Rico. The global conservation status of each individual species was reviewed, including geographic

range, as documented by herbarium specimens, supplemented with field observations from the experts. All species considered At Risk in either streamlined analysis were reviewed; any species considered Not At Risk in both analyses but considered to be of conservation concern by any of the experts were also included. All species provisionally assigned to one of the Red List Threatened categories under IUCN's Criterion B had an EOO less than 20,000 km² and also met two of three subcriteria (IUCN, 2001). Thus, the primary goal of the expert panel was to evaluate those species with restricted geographic ranges for the three possible subcriteria, fragmentation, decline, or fluctuation of known populations. For each species, experts' observations on numbers of known populations, numbers of available herbarium specimens, patterns of abundance, and numbers of individuals, when known by one or more panel members, was recorded.

Results

Results of the two streamlined analyses were previously reported (Miller et al., 2012), but in this review, the NY analysis was rerun with a much larger set of specimen data that recognized 2009 native seed plant species from Puerto Rico. Data from GBIF and NY were supplemented with herbarium specimen records from the three major Puerto Rican herbaria. The NY analysis identified 398 At Risk plant species, reduced from the 459 reported earlier (Miller et al., 2012), because of more adequate documentation of range and, therefore, greater EOO values resulting from the larger dataset and leading to fewer At Risk species. In the original NY analysis, it was not possible to calculate EOO for 142 species, which were known from fewer than three specimens, but with the larger dataset, it was possible to calculate EOO for all but 106 species, and the larger EOO values reduced the At Risk species by 62. The US analysis recognized 359 At Risk species, based on the original dataset (Miller et al., 2012). In total, 510 species were considered At Risk in one or the other analyses, and 247 of these were identified as such in both.

The results of the expert analysis to provisionally assign all species to the IUCN Red List categories are summarized in a table available on NY's website (<http://sweetgum.nybg.org/caribbean/J_Miller_et_al_Puerto_Rican_plant_conservation_status.pdf>). Species were considered Threatened when their calculated EOO was less than the 20,000 km² threshold for VU, and when experts' observations confirmed fragmented populations and likely decline in known populations or available habitat. The analysis identified 72 species as CR, 97 species as EN, and 86 species as VU, for a total of 255 Threatened species. In addition, 44 more species were identified as Near Threatened (NT), and 1710 species were considered Least Concern (LC). The two streamlined conservation analyses both proved very effective at predicting which species were considered Threatened by more detailed IUCN Red List analyses (Table 1). Both predicted all 72 species considered to be CR, the NY analysis predicted 96 (99%) and the US analysis 91 (94%) of 97 EN species, and the NY analysis predicted 82 (95%) and the US analysis 53 (62%) of 86 VU species. In total, the NY analysis predicted 250 (98%) and the US analysis 216 (85%) of 255 Threatened species, but the difference among the methods was not quite significant (chi square = 4.32, $df = 2$, $P = 0.12$). The NY analysis considered 148 more species At Risk, or 58% more than were not considered Threatened in the provisional IUCN listing. The US analysis identified 143 more species, or 56% more than were actually Red Listed. The three methods (the panel's assessment and the US and NY rapid assessment methods) did not differ significantly in the number of species assigned to the three categories (chi square = 5.71, $df = 4$, $P = 0.22$).

Table 1. Results of conservation analyses of Puerto Rican seed plants, contrasting provisional Red List category assignments with identification of species At Risk in the two streamlined conservation assessment methods. Provisional IUCN assignments were made by a local panel of experts. CR = Critically Endangered; EN = Endangered; VU = Vulnerable.

Provisional IUCN assignments	Streamlined assessment assignments		
	NY method	US method	
CR	72	72 (100%)	72 (100%)
EN	97	96 (99%)	91 (94%)
VU	86	82 (95%)	53 (62%)
Total (Threatened)	255	250 (98%)	216 (85%)

While each of the analyses was effective at identifying plants that would be considered Threatened by IUCN, they were even more effective when combined. The two analyses together identified all 169 CR and EN species and 83 of 86 species that IUCN would consider VU. In total, the combined analyses identified 99% of the species IUCN would consider Threatened. There were 258 species identified as At Risk in one or the other analyses that were not considered Threatened in the Red List

assignments, though 38 were among 44 species considered NT in the provisional Red List.

Discussion

It is clear that only a small percentage of the world's plant species have had their conservation status evaluated and that a streamlined, efficient process would help produce assessments in a timely manner that is responsive to the immediate threat that many species face. This study aimed to evaluate two methods that efficiently assess conservation status and used the flora of Puerto Rico as a test case.

Validation of the results of the two streamlined methods requires an assessment conducted by a method proven to produce credible results, against which the streamlined results can be compared. The panel of experts on the flora of Puerto Rico assembled at the University of Puerto Rico Botanical Garden in August 2011 used the IUCN guidelines (IUCN, 2001) to assess conservation status of all species potentially considered to be of conservation concern, under IUCN's criterion B. Geographic range has been considered a valid measure of conservation status in many previous studies (e.g., Gaston & Fuller, 2009) and is one of the five measures that IUCN accepts for Red List assignments (IUCN, 2001). The expert review assigned 12.7% of the flora to one of the three Threatened categories, which is less than the 20% or more estimated for most tropical floras (Pitman & Jorgensen, 2002; Brummitt et al., 2008), but quite similar to the 13.6% of the Puerto Rican flora considered to be endemic (Acevedo-Rodríguez & Strong, 2007). It is likely that the results of this analysis are conservative in the sense that they identify only those species for which restricted geographic ranges clearly document evident conservation concern, and in this analysis, 44 additional species were considered NT.

Comparison of the results from the two streamlined methods with the provisional Red List indicates that they were both excellent predictors of conservation concern, with the NY analysis identifying 250 (98%) of 255 Red List Threatened species and the US analysis identifying 216 (85%) of 255 Threatened species. The NY analysis identified an additional 148 species (58%) and the US analysis 143 species (56%) as At Risk, beyond those considered Threatened in the Red List analysis. No further analysis of the geographic ranges of these additional species were completed, but review of the information included in this analysis supports the assumption that the vast majority of species considered At Risk but not Threatened are species with restricted ranges and that are hence of some conservation concern. In fact, 44 of the additional species were considered NT in the Red List analysis.

The two methods did yield somewhat different results. The NY method predicted 98% of the Red List Threatened species as compared with only 85% by the US method. Given that the two methods evaluated here both use readily available data and can be completed efficiently, they can be a realistic approach to identifying the list of species needed to satisfy Target 2 of the GSPC, the same group of species that most desperately need conservation to ensure their near-term survival.

Conclusions

The most widely used system for assessing conservation status, the IUCN or IUCN's Red List system, has made only limited progress reviewing the conservation status of plants, providing assessments for fewer than 15,000 species, or only about 4% of the estimated seed plant species. Given this progress, it seems unlikely that the 2020 deadline for Target 2 of the GSPC, a list of the world's endangered plants, will be met. A streamlined system that can expedite review of the conservation status of individual species, using readily available data, is needed to rapidly compile the list of species that merits conservation attention. The two systems reviewed here, to assess the validity of the conservation assessments that they produce, are intended to provide the means to rapidly evaluate large numbers of plant species and achieve Target 2 of the GSPC. Used either individually or in tandem, these systems provide an efficient approximation of and a first step toward a Red List and could facilitate assessments rather than being an alternative system that would replace the Red List.

The congruence between the NY analysis and the provisional Red List assessments from the expert panel was very good, with the NY list of At Risk species including all but five, or 98%, of the species "Red Listed" as Threatened. The US analysis was not quite as effective, identifying only 85% of the Red Listed Species, 216 of 255. The provisional Red List was conservative in recognizing Threatened species, and both analyses identified significantly more At Risk species, 148 additional in the NY and 143 more in the US analyses. Given that the provisional Red List also included 44 NT species, and that most of the At Risk species are range restricted even if not sufficiently so to be considered Threatened in the Red List, the results of both analyses are very efficient at identifying Threatened species and the additional species they identify are almost certainly worthy of some conservation concern.

The two analyses combined were even more effective at identifying the Threatened species.

Given the efficiency at which the two tested methods evaluated the flora of Puerto Rico, using data that are readily available in internet-accessible databases, these methods could be very effective in evaluating the large numbers of species that will be necessary to reach Target 2 of the GSPC. Both methods require only a reliable checklist of the native plant species from the region to be evaluated (evaluations could also be organized taxonomically) and access to available herbarium specimen locality data. With the recent publication of checklists for Venezuela and Brazil (Hokche et al., 2008; <http://floradobrasil.jbrj.gov.br/2010/>) and pending checklists for Bolivia and Colombia (Jorgensen, in prep.; Bernal, in prep.), the only part of the New World not likely to have the necessary data available in the near future would be Mexico.

The two efficient analyses tested here both provide a means of realistically working to complete the assessments required to attain Target 2 of the GSPC. Furthermore, the list of species that they would generate would almost certainly contain nearly all of the species that would be identified as Threatened in a comprehensive Red List analysis, as well as a modest percentage of species that are range restricted, though not sufficiently to be considered Threatened. This list would be a decisive positive step toward completing a much greater number of Red List assessments, because it first essentially Green Lists a large percentage of species that IUCN would consider LC, and then allows labor for more complete analyses to be focused on the species that might possibly be of conservation concern. Furthermore, completing the analyses via the NY method focuses the most labor-intensive work, namely georeferencing those specimen records with locality data lacking geographic coordinates, on those species whose conservation status might actually be affected by redefinition of their geographic range. It is clear that some more efficient method will be required to achieve Target 2 of the GSPC, and the two methods presented here could both play a significant role in achieving that goal.

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FROM WORKING LIST TO ONLINE FLORA OF ALL KNOWN PLANTS—LOOKING FORWARD WITH HINDSIGHT[1]

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Abstract

The aim of this paper is to identify factors that might assist implementation of Target 1 for the Global Strategy for Plant Conservation (GSPC) for 2020: "an online flora of all known plants." This is done by considering progress in large regional floras to date and production of The Plant List online, in conjunction with lessons learned from the first 10 years of GSPC implementation. If the online flora is to support GSPC implementation, then it has to be able to support conservation and sustainable-use projects at national and local levels in addition to linking to information concerning global plant diversity. This will require strong partnerships and collaborations across the botanical community. Measurement of progress will help identify gaps and direct efforts, and indicators for measuring progress are suggested.

Key words: Flora, Global Strategy for Plant Conservation (GSPC), The Plant List, Targets.

The Global Strategy for Plant Conservation (GSPC) was adopted by the Conference of Parties (COP) of the Convention on Biological Diversity (CBD) in April 2002 (CBD, 2002). Target 1 ("a widely accessible working list of known plants species as a step towards a World Flora") was globally achieved on schedule on 29 December 2010 with the online launching of The Plant List (<www.theplantlist.org>). Ten years on from the original setting of Target 1, what lessons have we learned that can guide our responses and the implementation of the new Target 1 for 2020? As agreed at the 10th COP of the CBD in Nagoya, Japan, the revised Target 1 is "an online flora of all known plants" by 2020 (CBD, 2010a; <http://www.cbd.int/decision/cop/?id=12283>).

The Plant List

The Plant List was created to meet the 2010 Target 1 of the GSPC. This was a broad collaboration, coordinated by the Royal Botanic Gardens, Kew, and the Missouri Botanical Garden (MO), involving diverse partnerships. These extended from global data resources such as The International Compositae Alliance, which produced the Global Compositae Checklist (<http://compositae.landcareresearch.co.nz/>), the International Legume Database and Information Service (<http://www.ildis.org/>), to the International Plant Names Index (IPNI; <www.ipni.org>). Regional resources included various regional checklists held within the Tropicos database, including the African Plant Database (<www.ville-ge.ch/musinfo/bd/cjb/africa/index.php>), as well as contributions from many individuals. For example, over 155 collaborators from 22 countries have supported Kew's World Checklist of Selected Plant Families (WCSP; <www.kew.org/wcsp>).

The Plant List provides a working list of known plant species that aims to be comprehensive in coverage at species level for all names of mosses and liverworts and their allies (bryophytes), and for all names of vascular plants, which include the flowering plants (angiosperms), conifers, cycads and their allies (gymnosperms), as well as the ferns and their allies, including horsetails and club mosses (ferns and lycophytes). For each name at the species level, information in The Plant List includes the describing author(s) of the name, the original place of publication, and an assessment of whether the name is accepted in current taxonomic use or is a synonym for another name. For each name included, wherever possible, links are also provided to an online database record, to its corresponding entry in IPNI, and to any further sources of information about that plant taxon. For each name record, The Plant List indicates the level of confidence that the status of the name record is correct; the confidence assessments are based primarily on the nature and taxonomic

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integrity of the source data. Currently, The Plant List recognizes ca. 298,900 accepted names (28.7% of the total) and 477,601 synonyms (45.9%). There are 263,925 names unresolved for taxonomic status, which constitutes 25.4% of all names in Version 1 of The Plant List. This latter category represents work in progress because there was insufficient information held in the component data sets contributing to The Plant List to determine whether these names should be accepted or considered as synonyms of other names. The Plant List is a working list, and future versions are planned to improve the quality and to reduce the number of unresolved names. There are opportunities to broaden the network of collaborators supporting The Plant List, which should thus help to reduce the number of unresolved names and to improve the quality of data. In future versions of The Plant List, it will be important to further broaden the scope of institutional and individual collaborations to help improve the quality and long-term maintenance of the data.

Global Strategy for Plant Conservation (GSPC) Perspective—Strengths and Weaknesses

From a GSPC perspective, The Plant List could be viewed as a success in several ways. It was the result of a global partnership, illustrating how a clearly agreed upon target can focus the activities of interested parties, helping them to achieve a common objective. The process in constructing The Plant List demonstrated the importance of GSPC cross-cutting issues, such as the development of tools and methodologies (Target 3), and of strengthening networks and collaboration for plant conservation at national, regional, and international levels (Target 16; CBD, 2010a). However, it is a significant lesson for the implementation of the GSPC, generally, that the partners involved already had their business aims closely aligned to the Target (Paton & Nic Lughadha, 2011). The production of taxonomic checklists has long been one of the principal activities of taxonomic institutions, and the vast majority of contributors were engaged in activities complimentary to Target 1 before it was set. Target 1 provided a focal point for collaboration rather than driving larger-scale business change within the institutions involved.

An important aspect of enabling institutional and individual collaboration was the ability to monitor progress toward Target 1. Measures such as the number and families of taxa covered in component global checklists enabled a gap analysis to be conducted. In 2005, this analysis enabled the Global Biodiversity Information Facility (GBIF) to target these gaps in a call for proposals that resulted in the funding of two of these taxonomic gaps, for the Compositae (<http://compositae.landcareresearch.co.nz/>) and Melastomataceae (<www.melastomataceae.net/>; GBIF, 2005).

Although Target 1 for the GSPC in 2010 can be viewed as a success from a global perspective, the need for stronger implementation at a national level has been noted (CBD, 2008; Paton & Nic Lughadha, 2011). Capacity building at national levels as identified in the Global Taxonomy Initiative (GTI; <http://www.cbd.int/gti/>) and covered under Target 15 of the GSPC (CBD, 2010a) is important to ensure that a working list or online flora can be maintained to ensure that it supports national-level support and implementation of the CBD. Different countries will have different priorities and require different foci of taxonomic research and service. Capacity building is likely to remain a priority in the next 10 years of GSPC implementation, but such capacity-building initiatives need to have clear goals to support implementation of the convention (Paton & Nic Lughadha, 2011).

National-level input is vital for the long-term compilation and maintenance of a global working list or online flora. For this paper, an analysis (Paton, unpubl.) of the distribution of species covered by Kew's WCSP underlying database, which covers 173 families and 123,000 species (WCSP, 2012), was carried out. The WCSP provides Taxonomic Database Working Group (TDWG) level 3 distributions (Brummitt, 2001) for the species covered. This level corresponds to countries or parts of large countries such as the United States or China. The analysis found that 58% of seed plant species are only found in one TDWG level 3 area and, therefore, endemic to one country (WCSP, 2012). Thus, for the majority of seed plants, a national treatment will also be a global treatment. Generally, within the GSPC, there needs to be a stronger interplay between global resources, such as The Plant List, and national level resources (CBD, 2010b). This interplay will facilitate long-term maintenance of global resources and will ensure that national level resources maintain up-to-date knowledge concerning more widely distributed species that may cross national boundaries.

The GSPC Target 1 set in 2002 (CBD, 2002) provided a vision that extends well beyond 2010. Going forward to 2020, The Plant List and any other system used to support the assembly of an online flora needs to consider its long-term maintenance. Currently, The Plant List (Version 1, 2010) can be regarded as only a single picture at any given time. It is not maintained as a dynamic online resource, although this is a possibility in the future. At the moment, corrections are fed back to the collaborating

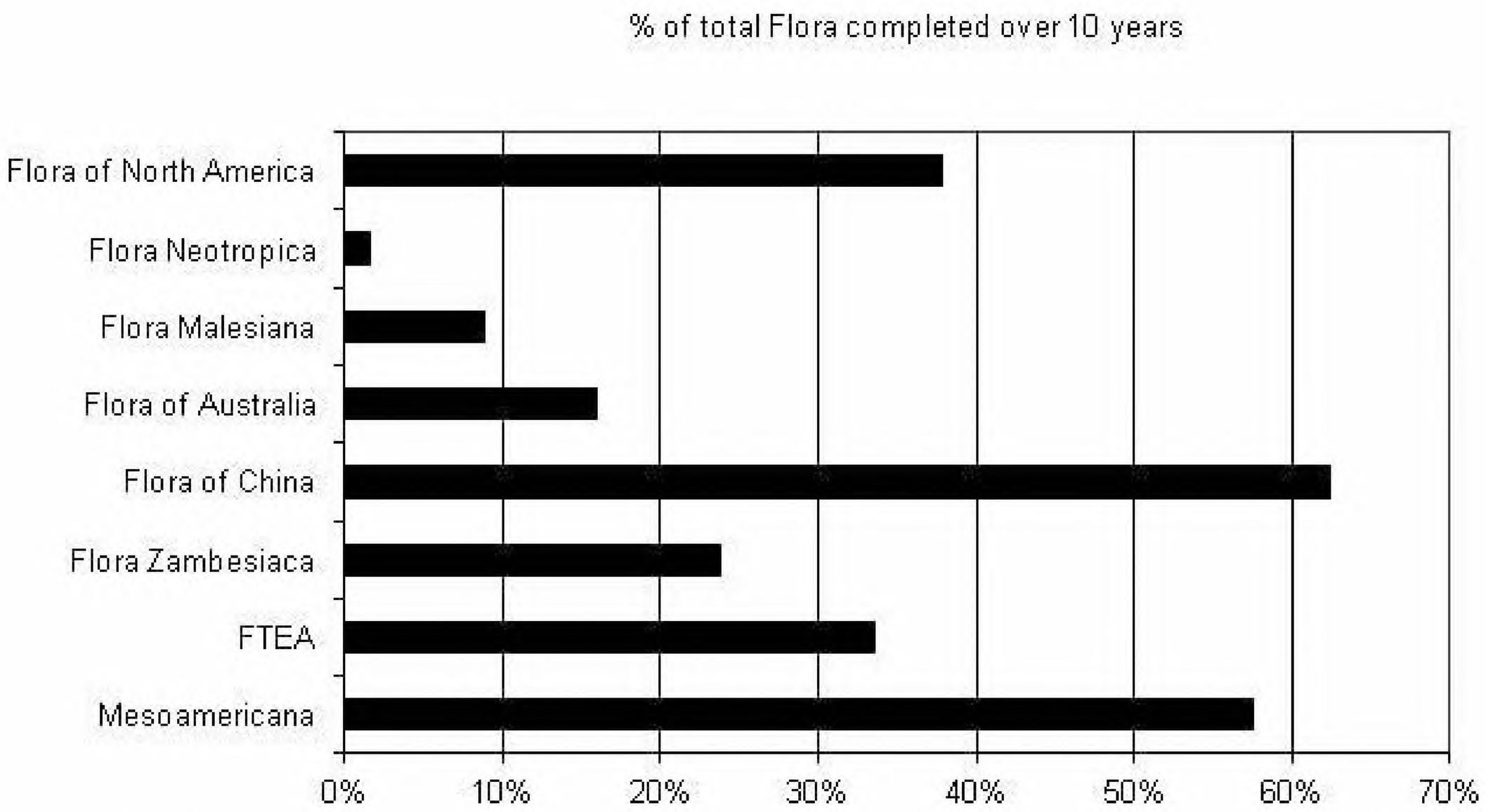


Figure 1. Progress in a selection of flora projects over the last 10 years. Totals from 2001 are taken from Heywood (2001). Results from 2012 come from the editors of regional or national flora projects asked to give totals for the number of species completed (see acknowledgments and Table 1 for details). Numbers reflect progress as of July 2012.

partner databases, and a planned new version of The Plant List will incorporate changes originating from these source databases. The lesson for GSPC implementation is that the processes used to achieve Target 1 on time may not be the most sustainable or efficient mechanisms to support implementation in the long term. Nevertheless, achieving the target of a working list for plant taxa worldwide is a vital first step toward an online flora.

The 2020 Target 1: An Online Flora of All Known Plants

It is important to clearly define what this online flora represents. This will enable potential partners to understand how best they can support work toward the current GSPC Target 1, and it will also facilitate monitoring and identification of gaps in implementation, which can then help further focus activities. For the 2010 Targets set by the COP Decision X/17 (CBD, 2010a), the definition of the first Target was initially provided by a rationale and description, which was then used as a basis for broader stakeholder consultation. Although the 2020 Target 1 has been agreed upon, with all 16 targets discussed at this workshop and the following liaison group meeting in St. Louis (CBD, 2011a), there is still opportunity for broader input from the scientific community who might implement the GSPC and policymakers. The aim here is to look at progress in large regional- or country-level floras to date in conjunction with lessons learned from the first 10 years of GSPC implementation and to identify factors that might assist implementation of Target 1 over the next 10 years.

Progress has been made in several large regional- or country-level floras over the last 10 years (Fig. 1; Table 1). Despite some impressive achievements, resulting in many species accounts being available for incorporation into an online global flora, none of these floristic projects were completed in a 10-year period. Nonetheless, the most impressive rates of progress were seen over the past decade for The Flora of China text series with 70% completion, Flora Mesoamericana with 57% completion, and the Flora of East Tropical Africa (FTEA) with around 34% of the known plant taxa treated. It is apparent that progress in larger regional areas, e.g., the Flora Malesiana and Flora Neotropica, tends to be slower than that in large country-driven projects such as Australia and China or in smaller regions such as the FTEA and Flora Mesoamericana; although, it should also be noted that monographs play an important role in covering plant groups from larger areas such as the Neotropics (Thomas, 1999). However, there is an important difference in the information content of traditional floras or monographs as contrasted with an online flora that meets Target 1 of the GSPC and supports the other 15 specific targets as well as the implementation of the CBD, generally. An online

Table 1. Progress in a selection of regional or national flora projects over the last 10 years. Totals from 2001 are taken from Heywood (2001). Results from 2012 come from editors of the flora projects asked to give totals for the number of species completed (see acknowledgments). Numbers reflect progress as of July 2012. In the New World, the Flora of North America treats plant taxa from the United States and Canada; the Flora Mesoamericana considers plants from Mexico south through Panama, and treatments in the Flora Neotropica extend to the south through Peru, Bolivia, and Uruguay. Plants of the African continent are investigated by the Flora of East Tropical Africa and the Flora Zambesiaca (Botswana, Malawi, Mozambique, Zambia, Zimbabwe, and the Caprivi Strip). The remaining projects treat plant taxa in China and Australasia, with the Flora Malesiana, which includes the following countries: Indonesia, Malaysia, Singapore, Brunei Darussalam, the Philippines, and Papua New Guinea in southeastern Asia.

	Species completed 2001	Species completed 2012	% Complete 2001	% Complete 2012	% Completed since 2001	Estimated total number of species
Flora Mesoamericana	3249	13,412	18%	76%	57%	17,683
Flora of Tropical East Africa (FTEA)	12,104	12,104	66%	100%	34%	12,104
Flora Zambesiaca	5960	8417	57%	80%	23%	10,528
Flora of China	9642	29,232	31%	93%	62%	31,360
Flora of Australia	6369	9452	33%	49%	16%	19,306
Flora Malesiana	8000	11,750	19%	28%	9%	42,500
Flora Neotropica	6237	7715	7%	9%	2%	90,000
Flora of North America	3249	11,004	16%	54%	38%	20,500

world flora that supports CBD implementation will need to present or link to broader information; otherwise, the Target will not support the implementation of the convention (Table 2). Given current rates of completion and requirement for additional information, clearly floristic writing as usual will not provide an online global flora that fully supports the implementation of the GSPC and the CBD by 2020.

Looking Ahead with Hindsight

The GSPC implementation has been reviewed at different times and from different perspectives. Such reviews include the Third National Reports of Parties to the CBD (<http://www.cbd.int/reports/analyzer.shtml>); an in-depth review of the implementation of the GSPC was considered by the Subsidiary Body on Scientific, Technical, and Technological Advice (SBSTTA) at their 12th meeting in Paris in June 2007 (CBD, 2007); and by the Conference of the Parties to the CBD at their ninth meeting (COP IX) in Bonn, Germany, May 2008, as reflected by the decisions arising there (CBD, 2008). This was followed by the CBD Plant Conservation Report issued by the Secretariat of the CBD (SCBD, 2009); and an online consultation and recent review of implementation in botanic gardens (Williams & Sharrock, 2010). The findings of these reviews were compared and contrasted by Paton and Nic Lughadha (2011). The factors found to be associated with successful implementation of the GSPC included: (1) the targets having a clear focus with identified outcomes and a degree of flexibility in how these outcomes were achieved; (2) a core group of stakeholders acting as a community and sharing similar business aims; and (3) a mechanism for monitoring progress and identifying gaps. How might these factors influence development of the online flora of all known plant species?

Focus and Flexibility

As seen in Table 2, a flora traditionally covers a broad range of taxonomic, geographic, and nomenclatural information, yet an online flora that supports other targets of the GSPC (Targets 2, 7, 9–13; cf. Table 2) would cover an even broader range of information. One way to speed up the production of significant regional and country floras as well as The Plant List is to ask what is the minimum requirement for floristic treatments? This might be as simple as the provision of an accepted name of a taxon and its synonymous names to clarify what species exist and then what names have been used historically to recognize the taxon. As the CBD is implemented at a national level, it would be important to include, in a minimal view, country-level distributions so that country inventories could easily feed into and receive information from such an accepted plant name and distribution backbone. Such a minimal backbone for names of known plant taxa and their country-level geography would provide a clear focus for the GSPC Target 1, but also the flexibility to link and add further information to it. A similar approach was recently discussed at the 16th meeting of SBSTTA (CBD, 2012a). Existing descriptions, illustrations, and distributional detail could be linked to a taxon's record without the need for standardized text or

Table 2. Summary of the taxonomic information found commonly in traditional floras. This is contrasted with taxon information required to support implementation of other Targets (2, 7, 9–13)[1] of the Global Strategy for Plant Conservation beyond Target 1, which seeks "an online flora of all known plants" (Convention on Biological Diversity [CBD], 2010a).

Taxon information for traditional floras and Target 1	Additional taxon-level information supporting other targets
Accepted name	Conservation status (Target 2)
Synonyms	Genetic diversity (all Targets)
Description	Economic Use (Targets 11–13)
Identification key	Medicinal use (Targets 11–13)
Illustrations	Invasive potential (Target 10)
Distribution	Trade statistics, nondetriment information for CITES implementation (Target 11)
Relationships	Traditional uses (Targets 7, 9, 13)
Phylogeny	Common names (all Targets)
Literature citations	
Specimen and type citations	

[1] Additional Targets (CBD, 2010a). Target 2: An assessment of the conservation status of all known plant species, as far as possible, to guide conservation action. Target 7: At least 75 per cent of known threatened plant species conserved in situ. Target 9: Seventy per cent of the genetic diversity of crops, including their wild relatives and other socio-economically valuable plant species conserved, while respecting, preserving and maintaining associated indigenous and local knowledge. Target 10: Effective management plans in place to prevent new biological invasions and to manage important areas for plant diversity that are invaded. Target 11: No species of wild flora endangered by international trade. Target 12: All wild harvested plant-based products sourced sustainably. Target 13: Indigenous and local knowledge innovations and practices associated with plant resources maintained or increased, as appropriate, to support customary use, sustainable livelihoods, local food security and health care.

descriptive language as required by an established, traditional flora format. Other information integral to conservation, such as threat assessment, harvesting information, or a plant's invasive potential, could also be linked to such an initial backbone toward a global flora. An important element of any flora is a key to aid identification. However, keys to plant taxa do not need to operate at a global level. Existing country- or regional-level keys could be linked to a family and genus hierarchy. New and existing keys could be contributed to IdentifyLife (<www.identifylife.org>), thus benefiting from existing information and facilitating other key-building activities.

These elements could build directly on a backbone of scientific names for accepted, known plant taxa such as The Plant List, although a more sustainable system would have to be developed in order to keep the data and links up to date, and an inclusive system of editors would have to be developed to help maintain the system. Currently, The Plant List is static and cannot be edited online. There are successful examples of plant specialist communities maintaining data in online taxonomic systems, for example, the Solanaceae Source (<www.solanaceaesource.org>) and eMonocot (<http://e-monocot.org/>). Not every taxonomic group will have such a broad-based community to support its e-taxonomy, but more open, community-based collaborations will greatly facilitate taxonomic progress (Knapp, 2008) and achievement of the GSPC Target 1.

COMMUNITY SUPPORT: STAKEHOLDERS ACTING AS A COMMUNITY AND SHARING SIMILAR BUSINESS AIMS

The Plant List provides a names backbone, as discussed above, and includes detail from both regional datasets and global datasets. Monographic datasets that treat taxa globally have the advantage of providing a logically consistent view of the taxonomy for any area, whereas regional datasets may differ in their treatment of particular taxa, creating problems when these regional datasets are combined. It is likely that a flora of all known species would be composed of elements derived from both regional and monographic databases. Relatively few new data resources covering single large plant families have been developed over the last 10 years, the exceptions being the Compositae and Melastomataceae as previously mentioned. Ten large plant families that lack comprehensive or global species treatments or a database are shown in Table 3. Several of these larger families with significant taxonomic gaps have portions completed, e.g., in Apocynaceae, but global communities of plant specialists have not yet committed to the support necessary to maintain comprehensive databases for these families. This may be because the involved scientists have narrower taxonomic interests, as in the case of Apocynaceae where the subfamilies Apocynoideae and Rauvolfoideae have been reasonably, completely treated, but Asclepiadoideae, Periplocoideae, and Secamonoideae lag behind (WCSP, 2012). For other large families (cf. Table 3), funding or available specialists

Table 3. Families of vascular plants with over 2500 species that are not yet covered by a global species checklist.

Plant family	Estimated species number
Apocynaceae	4552
Malvaceae	4225
Ericaceae	3995
Apiaceae	3780
Acanthaceae	3500
Boraginaceae	2740
Urticaceae	2625
Ranunculaceae	2525
Amaranthaceae	2500
Lauraceae	2500

have not been available to complete treatments comprehensively across the family, e.g., Amaranthaceae. In other instances, taxonomists may be more interested in geographic or generic levels rather than family ones, as in Ericaceae. In both instances, energy necessary to pull the community together to produce this list has not been provided. Recent experience suggests that there are two means whereby global communities have been catalyzed to come together to produce a global checklist: (1) external funding as in the case of GBIF-funded projects (e.g., GBIF, 2005); and (2) draft electronic checklists being compiled from the literature and existing resources with expert communities then reviewing the list product, as in the case of those families covered by the WSCP (Paton et al., 2008; WSCP, 2012).

Regional- or national-level input into an online world flora will be important not only to fill the gaps among global species databases for particular families, but also to help maintain them and improve their quality. Broad participation will be vital for the long-term success of the GSPC. In terms of the GSPC Target 1 and the production of an online flora, those contributing to it must receive professional recognition for their efforts. The lack of accreditation for those compiling global checklists has been and still is a major barrier to completing a working list of known species (Paton et al., 2008). However, research councils are now considering such impacts as part of their research assessments. Projects such as the European Union–funded Virtual Biodiversity Research and Access Network for Taxonomy (ViBRANT; <http://vbrant.eu/>) focus on the development of virtual research communities involved in biodiversity science and must consider ways in which such online contributions can be recognized by the broader scientific community and funding sources. Objective measures of research impact and the value of contributions to an online flora will be easier to provide if the online flora connects to conservation and sustainable use information essential to those implementing the convention on the ground. Such linkages will boost the use and citations of the online flora and any associated data contributions.

MEASURING SUCCESS

As noted above, having a mechanism to monitor progress toward the target and to identify taxonomic gaps was an important factor in progress toward Target 1's working list prior to 2010. For the GSPC, such general monitoring of progress needs to be linked to the Aichi Biodiversity Targets (<www.cbd.int/sp/targets/>), both to demonstrate how the GSPC supports the strategic plan of the CBD and also to integrate monitoring and reporting with other environmental initiatives (CBD, 2011a). Otherwise, the report burden from different conservation or sustainable management initiatives constitutes a barrier to the acceptance and fulfillment of the targets (CBD, 2010a). The ways in which GSPC Targets support the Aichi Biodiversity Targets have been outlined by the Liaison Group on the GSPC (CBD, 2011a). The GSPC Target 1 is most relevant to the Aichi Biodiversity Target 19: "By 2020, knowledge, the science base and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied." Just as Target 1 underpins the other 15 GSPC Targets, it is also relevant to many of the other Aichi Biodiversity Targets, and a process is underway to develop indicators for the Aichi Biodiversity Targets. A set of headline indicators has been developed, under which operational indicators or metrics are then organized. The most relevant headline indicator to the GSPC Target 1 being "trends in accessibility of scientific/technical/traditional knowledge and its application" (CBD, 2011b). Underneath this, operational indicators apply at both global and subglobal levels, the most relevant to Target 1 address: (1) "trends in coverage of comprehensive policy-relevant sub-global assessments including related capacity building and knowledge transfer, plus trends in uptake into policy"; and (2) "number of maintained species inventories being used to implement the Convention." This second indicator reflects discussion within the Coordination Mechanism (CBD, 2011d) for the GTI concerning the need to have an indicator that reflected the importance of taxonomy underpinning the CBD and other environmental agreements (CBD, 2011c).

The Aichi Biodiversity Targets and their suggested indicators provide a mechanism for monitoring the

implementation and impact of the environmental agreements such as the CBD, and to a less precise extent, to components programs such as the GSPC or GTI. However, to monitor progress and identify gaps in the implementation of the 16 GSPC Targets, more granular measures will be required. Such measures of progress for individual targets should be part of the GSPC tool kit (CBD, 2012b; <http://www.plants2020.net/>) to be developed to support implementation at both national and regional levels (CBD, 2010a). For Target 1, measures to help monitor progress will need to be developed. Such measures should cover:

(1) Taxonomic completeness. Unresolved scientific names should steadily decrease over time and, concomitantly, confidence should build in those names as peer-reviewed taxonomic decisions similarly increase. For example, in The Plant List, there should be a decrease in the number of unresolved names and an increase in the confidence ratings on the placement of names as accepted or synonyms over time.

(2) Links to additional information. As the online global flora develops, the numbers of accepted names with links to additional information necessary to implement the CBD should increase. Such additional information could include plant images, description, geographic distributions, and common names and coverage in taxonomic keys to aid identification. The number of linkages to support other targets of the GSPC could also be measured, e.g., an increasing number of conservation assessments, which would link to the GSPC Target 2, which notes "[a]n assessment of the conservation status of all known plants species, as far as possible, to guide conservation action."

(3) Support and participation. Measurable assessments toward progress of a global flora could be demonstrated by an increase in the number of countries supplying information to an online flora. Also pertinent would be the broadening distribution of contributing taxonomists and other committed individual scientists. As elsewhere in the scientific community, the number of citations of the online flora content would offer measureable progress toward widespread acceptance of the 2020 goal for the GSPC Target 1 toward the accomplishment of an online global flora.

Conclusion

If the online flora is to support GSPC implementation, then this Target 1 must also support conservation and sustainable-use projects at national and local levels, beyond providing or acting as a link to information concerning global plant diversity. To fulfill these functions, the online global flora should be complete and of sufficiently high quality such that information about plants can be found with confidence. Target 1 must link to information of use to those working in conservation and sustainable use at national and regional levels, and an online global flora must be supported by a broad range of stakeholders who can help to maintain and to update its taxonomic and other essential databases. Previous reviews have demonstrated that being able to monitor progress has assisted implementation of the GSPC Target 1 (Paton & Nic Lughadha, 2011), and it will be important to monitor progress using measures such as those detailed above.

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IN VITRO METHODS AND THE CHALLENGE OF EXCEPTIONAL SPECIES FOR TARGET 8 OF THE GLOBAL STRATEGY FOR PLANT CONSERVATION[1]

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ABSTRACT

For the majority of plant species of conservation concern, seed banking and traditional propagation methods are the most efficient ways of meeting the ex situ and recovery conservation goals of Global Strategy for Plant Conservation (GSPC) Target 8. However, there are estimated to be 5000 or more endangered species for which these methods will not be adequate conservation tools. These "exceptional" species are those with recalcitrant seeds or those that produce few or no seeds. In vitro methods can provide alternative procedures for propagating and preserving germplasm in the long term for these species. Research at the Center for Conservation and Research of Endangered Wildlife (CREW) with several U.S. endangered species has shown the potential of these methods. In vitro propagation can provide plants for reintroduction and research when traditional propagation methods are not adequate. Phytotissue banking can be used for long-term ex situ conservation when seed or embryo banking is not possible. In vitro methods are also needed for recovery when embryo banking of recalcitrant seeds is possible. The full implementation of in vitro methods is constrained by information, scientific, and economic challenges, but the need for its use in meeting the needs of exceptional species should provide impetus for overcoming these challenges and making these methods an integral part of an overall ex situ conservation strategy.

Key words: Cryopreservation, ex situ conservation, Global Strategy for Plant Conservation (GSPC), in vitro, tissue culture.

Ex situ conservation has become a major tool for plant conservation. As such, it is one of the major targets of the Global Strategy for Plant Conservation (GSPC). Target 8 states: "At least 75 per cent of threatened plant species in ex situ collections, preferably in the country of origin, and at least 20 per cent available for recovery and restoration programmes" (Convention on Biological Diversity [CBD], 2011). This goal is primarily accomplished through seed banking, which, for most species, provides the most efficient method for long-term preservation of multiple genotypes. However, there is a subset of endangered species for which seed banking is not workable, including species with recalcitrant seeds (desiccation-sensitive seeds that cannot survive traditional seed banking protocols) and a significant number of species that produce few or no seeds, or for which seed collection is not practical. Combined, these form a group of unbankable or "exceptional" species that may comprise an estimated 5000 to 10,000 plant species of conservation concern (Pence, 2011a). Because exceptional species are fewer in number than species with available, bankable seeds, and because they require more costly approaches to ex situ conservation, they are more likely to be overlooked as a group. However, these exceptional species are just as likely, if not more so, to hold potential value, since many are components of species-rich and ecologically complex tropical rainforests. Thus, it is important to consider the challenges posed by this group for conservation biologists and to evaluate what is needed for dealing with them.

IN VITRO TOOLS IN EX SITU CONSERVATION AND RESTORATION

Many of the tools available for dealing with the ex situ conservation and propagation of exceptional species include at least some aspects of in vitro culture, and the extent to which this biotechnology is needed will influence the labor and resources required for a particular species (Pence, 2011a, 2011b). For example, excised embryo axes from recalcitrant seeds, such as the endangered Texas wild-rice *Zizania texana* Hitchc. and the common horse chestnut, *Aesculus hippocastanum* L., have been shown to survive rapid freezing in liquid nitrogen (Wesley-Smith et al., 2001; Walters et al., 2002). This allows the cryobanking of multiple genotypes in one sample, as is the case with intact

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seeds. However, this requires the excision of embryos prior to banking followed by the recovery of the embryos using in vitro systems, thereby increasing the input of labor and resources compared with seed banking. Another approach is the cryopreservation of dormant buds in woody taxa, which has been demonstrated with cold-hardy and cold-acclimated tissues (Towill & Ellis, 2008). With some plant species, such as willows (*Salix* L.) and apples (*Malus* Mill.), recovery can be accomplished through bud grafting or direct rooting (Forsline et al., 1998; Towill & Widrlechner, 2004), while in vitro methods have been used in persimmon *Diospyros kaki* Thunb. for post-freezing recovery growth (Matsumoto et al., 2001). If embryo axes or buds of an exceptional species cannot be cryopreserved, tissue banking using in vitro methods may be the more effective route for securing germplasm ex situ.

In vitro tools for conservation and restoration are based on the growth of plant tissues in tissue culture, a flexible technique that can adapt to a variety of needs (George & Debergh, 2008). The primary requirement for ex situ conservation is that plants can be recovered for restoration needs. Shoot propagating cultures and somatic embryo cultures are both capable of producing plants in vitro that can be acclimatized to soil and used for restoration. Shoot tips and embryogenic cultures have also been used for cryopreserving tissues long term in liquid nitrogen (Lombardi et al., 2008; Reed, 2008a), and thus, these have been the primary types of cultures used in conservation efforts.

In vitro propagation protocols have been described for hundreds of plant species, many of which are of economic importance, but some protocols have been developed for endangered taxa, such as several from Australia, Spain, and Hawaii (Bunn, 2003; Gonzalez-Benito & Martin, 2011; Sugii, 2011). In vitro methods can assist plant conservation starting at the point of a taxon's collection. The technique of in vitro collecting can be used to initiate tissue cultures in the field, when seeds or cuttings are unavailable or unworkable (Pence & Engelmann, 2011). In vitro propagation can be used to maintain ex situ collections, as is being done for native Brazilian vascular taxa (Pilatti et al., 2011) and for European bryophytes (Rowntree et al., 2011). Tissue culture can also be used to produce plants for restoration, as has been done with the Autumn buttercup *Ranunculus aestivalis* (L. D. Benson) Van Buren & K. T. Harper and the Cumberland sandwort *Minuartia cumberlandensis* (Wofford & Kral) McNeill. Both are two endangered species in the United States that have been propagated through tissue culture and outplanted in Utah and Kentucky, respectively (Pence et al., 2008a, 2008b). By using in vitro propagated plants, restoration experiments can be conducted without loss of genetic material, since back-up material of each clonally propagated line can be maintained in the lab, either as an active culture or as cryopreserved tissue. This may be particularly useful in seeking out new habitat if assisted migration experiments are undertaken with exceptional species (Vitt et al., 2010).

In vitro cultures can also provide material for cryopreserving tissues for long-term ex situ storage (Engelmann, 2011). While fewer species have been cryopreserved, compared with those propagated in vitro, liquid nitrogen storage has been a valuable tool for maintaining germplasm of rare plant taxa, particularly those classified as exceptional species. Tissue cryopreservation has been vital for the ex situ conservation of the federally listed Todson's pennyroyal, *Hedeoma todsenii* R. S. Irving, from New Mexico, for which seed production has never been observed (Pence et al., 2009). Species management utilizing long-term storage in liquid nitrogen has been effectively used across major plant groups ranging from European bryophytes (Rowntree et al., 2011) to vascular plants under threat in the native Australian flora (Kacmarczyk et al., 2011). Several basic methods are available and cryopreservation appears to be adaptable to a wide range of plant species (Reed, 2008a), although methods often need to be adjusted for particular species and genotypic variations. As with in vitro propagation, work with a related but common species can often facilitate protocol development for rarer species (Turner et al., 2001).

Challenges for the Application of In Vitro Methods

It is clear that in vitro tools allow us to go beyond the limits of traditional seed banking to include exceptional species in conservation efforts, making it possible to include, in theory, almost all plant species within the focus of Target 8 of the GSPC. Work in translating this theory into practice, however, faces at least three challenges.

The Information Challenge

Fundamental to addressing the needs of exceptional species is the challenge of identifying those species and determining the most effective and efficient methods for their conservation. While it is possible to develop a rough estimate of the number of exceptional species that may exist (Pence, 2011a), identifying them for specific conservation efforts will

require at least three levels of information. The first requirement is the comprehensive listing of all plant species set as Target 1 of the GSPC. This has been largely completed with ongoing updates by the Missouri Botanical Garden and the Royal Botanic Gardens, Kew, and can be accessed online (The Plant List, 2010). Second, within this list, species that are of conservation concern must be identified, as defined in Target 2 of the GSPC. Work on this has been conducted on many fronts, as Red Lists have been compiled, often at regional or national levels. The global effort is spearheaded by the International Union for Conservation of Nature and Natural Resources (IUCN, 2011) and is in progress.

Finally, the third need is to define for each endangered species the most appropriate methods for achieving the ex situ conservation and restoration goals of Target 8 of the GSPC. This is the most challenging level of information to acquire, since this requires an evaluation of whether the species can be stored conventionally or is an exceptional species. Some of this information is becoming available as species are described in national or regional lists of endangered plants, such as in the Plant Profiles for the Center for Plant Conservation's (CPC) National Collection of Endangered Plants (CPC, 2012). Information on seed characteristics for both endangered and non-endangered species is also being compiled in the Seed Information Database (Royal Botanic Gardens Kew, 2008). However, because this will depend on having a completed list of endangered plant species and will require the individual evaluation of each of those species, a full listing of endangered exceptional species is not yet available.

Despite this lack of information, many species are already known that fall into the exceptional category, and some of these are known to be endangered (CPC, 2012). Methods for tissue banking have been applied to several exceptional species in this laboratory to examine the logistics and costs of dealing with cryopreserving multiple genotypes for ex situ conservation (Pence et al., 2009; unpubl.). These species include three federally endangered exceptional species: the fourpetal pawpaw, *Asimina tetramera* Small, and Avon Park rattlebox, *Crotalaria avonensis* DeLaney & Wunderlin, which are both found in the state of Florida, as well as Todsen's false pennyroyal, *Hedeoma todsenii*, from New Mexico. Species that are already known as exceptional can serve as models for evaluating and refining methods that can then be applied to the larger group of species, yet to be identified.

SCIENTIFIC CHALLENGES

Plant tissue culture, while firmly based in the science of plant physiology and development, still encompasses a wide range of variability between species and often among genotypes. Developing protocols for species new to tissue culture is normal for those wishing to use in vitro methods for plant conservation. Some species respond easily to commonly used protocols (George & Debergh, 2008), while other taxa may prove recalcitrant to one or more of the steps necessary to culture the plant and return it to ex vitro conditions. Species may be difficult to initiate into culture due to internal contamination, excessive production of phenolic compounds, or unusually slow growth. Shoots may be difficult to root; somatic embryos may not develop into normal plants in vitro; and plants may not acclimatize easily from culture to soil substrates (Benson, 2000; Bunn, 2003; Bunn et al., 2011). All of these may be points of challenge, depending on the species. Even closely related species and genotypes within a single exceptional species can be more or less amenable to the various steps of culture (Reed, 2008b; Uchenda & Reed, 2008). The goal of any in vitro work with an endangered taxon is to efficiently and effectively move it into culture, to preserve plant tissue, and ultimately to propagate plants from in vitro cultures for restoration projects. While this is rarely achieved with ease, there are species that can serve as models for directions that researchers might explore in dealing with more difficult species.

Species of *Saintpaulia* H. Wendl., or African violets, are endangered in their native habitat of southern Kenya and northern Tanzania (Eastwood et al., 1998), despite the fact that *Saintpaulia* hybrids are common worldwide as houseplants. *Saintpaulia* is easily propagated, even without tissue culture intervention, but in vitro propagation can provide plants free from pests and diseases that might be more suitable for restoration projects than conventionally propagated plants. In vitro cultures can also provide material for tissue cryopreservation and banking when seeds are not available at the time that a wild habitat site is visited. *Saintpaulia* leaves will survive several days of common postal transport or courier, and thus, leaves can be collected and sent to a distant lab for culture. *Saintpaulia* shoots can be regenerated from leaf tissue using several media formulations. These shoots root easily in culture and the resulting plants acclimatize readily (e.g., Cooke, 1977; Mithila et al., 2003; Khan et al., 2007). Shoot tips from in vitro cultures of commercial cultivars of *S. ionantha* H. Wendl., originally native to Tanzania and Kenya, have been shown to

survive three of the standard cryopreservation protocols (Moges et al., 2004). Normally, one of the most labor-intensive steps in shoot tip cryopreservation is the dissection of the many small shoot tips needed. However, with *Saintpaulia* on some hormonal combinations, many small buds form as clusters on the cut margins of cultured *Saintpaulia* leaves. We have found that shoot clusters can be scraped from the leaf surface with a scalpel, cut into smaller pieces, and then subjected to cryopreservation procedures. While each meristem is not completely delineated in this system, the growing points are small enough and numerous enough to provide material that can survive liquid nitrogen exposure and later regrow (Fig. 1). Such a system greatly reduces dissection time and, consequently, the labor involved in cryopreservation protocols. The ability to manipulate growth in vitro in other species to provide similar tissue for cryopreservation could help facilitate the ex situ conservation of exceptional species.

An approach that has been commonly used when dealing with new species in culture is to use information from the culture of related, but non-endangered species to guide the development of new protocols. This approach was used in recent work with four endangered oak (*Quercus* L.) species from the United States. Methods used in other laboratories to initiate cultures and produce shoots and somatic embryos with several nonthreatened species ultimately proved successful with three of four species tested that were new to culture, *Q. arkansana* Sarg., *Q. boyntonii* Beadle, and *Q. georgiana* M. A. Curtis (Kramer & Pence, 2012). However, this approach may not always be possible, as many endangered species do not have congeners that have been grown in vitro, and families with high numbers of endangered species have not always been prioritized for in vitro studies (Pence, 2011b). Other avenues could also prove helpful. Natural adaptations have been recognized as an important consideration in developing cryopreservation protocols (Benson, 2008), and these may also prove to be important in developing in vitro propagation protocols for species new to culture.

THE CHALLENGE OF COSTS

The third major challenge for efforts directed at meeting Target 8 for exceptional species is the cumulative cost, a factor closely linked to the information and scientific challenges described above. This subject has been discussed in more detail elsewhere (Pence, 2011a), but in general, labor is the primary cost for protocols involving in vitro methods. While the costs are always likely to be higher than seed banking and traditional propagation methods, the more readily a species is initiated into culture, cryopreserved, and propagated, the less expensive those efforts will be. Information on the requirements of individual species is also critical, as different exceptional species will require varying levels of attention. For example, species that can be banked as isolated embryos will avoid the costs of initiating an in vitro culture before cryopreservation and will include multiple genotypes in a single banking exercise. Species requiring tissue banking must be initiated into culture, cryopreserved as multiple genetic lines, and recovered in vitro, thereby increasing efforts and costs. However, once banked, maintenance costs for tissues or embryos in liquid nitrogen are lower than maintaining species as active in vitro cultures or in living collections and do compare favorably with seed banking (Epperson, 1997; Reed et al., 2004; Keller et al., 2008; Li & Pritchard, 2009).

Meeting the increased costs of propagating and preserving exceptional species will benefit from multiple levels of collaboration and coordination. Academia, nonprofit organizations, government, and industry all have expertise and infrastructure that might be utilized in meeting Target 8 for exceptional species by contributing to basic research, protocol development, and actual banking or propagation activities. Over the long term, the cost of banking and maintaining endangered exceptional species ex situ will be significantly lower than the costs of comparably maintaining ex situ living collections of endangered animals, but the costs for exceptional species as a group will likely be measured in millions of dollars (Pence, 2011a). The challenge of these costs will best be minimized by creatively using multiple partners, coordinating information and effort, harnessing basic research, and leveraging monetary funding with in-kind support.

CONCLUSIONS

Exceptional species, or those without bankable seeds, pose a significant challenge to meeting Target 8 of the GSPC. Representing perhaps 5% or less of all endangered species, the goal in Target 8 of "at least 75 per cent of all threatened plant species in ex situ collections," and "at least 20 per cent available for recovery and restoration programmes" (CBD, 2010; Sharrock et al., 2010) could be met by not including any exceptional species. However, the worth of a species to humankind and to the environment cannot be determined by its ability to conform to traditional ex situ conservation methods.



Figure 1. —A. *Saintpaulia* plant growing in Tanzania. Photo by Johanna Kolehmainen. —B. Adventitious buds of *Saintpaulia ionantha* H. Wendl. subsp. *rupicola* (B. L. Burtt) I. Darbysh. forming on leaf cultured in vitro. —C. Cryopreserved buds of *S. ionantha* subsp. *grandifolia* (B. L. Burtt) I. Darbysh. growing into small plants on recovery medium. This culture was from African violet stock that originally came from Tanzania. Images taken by V. C. Pence at the Center for Conservation and Research of Endangered Wildlife (CREW).

Thus, consideration needs to be given to what resources and approaches are needed to include highly threatened exceptional as well as conventional species in efforts to achieve Target 8.

This challenge needs to be met by the use of alternative tools, including in vitro methods, but will require information that identifies the needs of particular species for these tools. The effective use of in vitro methods will also require further research into the basic science of manipulating plants in tissue culture as well as the development of coordinated collaboration between multiple partners with complementary skill sets, in order to most effectively and efficiently utilize existing expertise and infrastructure. These challenges are significant, but the need for conserving all endangered plant species mandates that they be addressed. By identifying and understanding these challenges, they will be more easily evaluated and integrated into strategies for the ex situ conservation and restoration of all rare plant species into the future.

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LESSONS FROM THE CONSERVATION ASSESSMENT OF THE SOUTH AFRICAN MEGAFLORA[1]

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ABSTRACT

South Africa has the world's richest temperate flora, with 20,456 indigenous vascular plant taxa recorded. With the current estimate of the global flora at 379,881 taxa, 5% of the world's plant diversity is represented within South African borders. Between 2004 and 2008, South African botanists completed a comprehensive assessment of the status of the South African flora using the International Union for Conservation of Nature and Natural Resources (IUCN) Red List categories and criteria, version 3.1. South Africa is the first floristically megadiverse country to fully assess the status of its entire flora and to achieve Target 2 of the Global Strategy for Plant Conservation (GSPC): "[a]n assessment of the conservation status of all known plant species, as far as possible, to guide conservation action." Herein, we discuss the critical success factors that allowed an assessment of such a megadiverse flora within five years. Establishing a centralized team of ecologists to develop Red Lists, collaborating with a wide range of botanical experts, streamlining the assessment process via automation, and establishing a data management system that served local conservation needs were crucial to the success of the project. Utilizing the IUCN categories and criteria proved to be, and is suggested as, the most cost-effective measure for other megadiverse countries wanting to achieve Target 2. Quantitative assessments can be done with minimal data, and comprehensive assessments of all known taxa ensure conservation attention for a greater proportion of a flora. The example of South Africa demonstrates that conservation assessments can be done relatively cheaply in developing megadiverse countries (less than $30 per taxon for South Africa). As megadiverse countries have high numbers of endemic plant taxa, it is well worth the investment by IUCN and conservation donors to support continued and future assessment projects.

Key words: Conservation assessments, Global Plant Conservation Strategy Target 2, IUCN Red List, South African flora, threatened species.

There is a global imperative to assess the conservation status of plant species to improve and measure conservation efforts. Currently, vascular plants worldwide are poorly represented on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species (Krupnick et al., 2009; Stuart et al., 2010), and only 15,190 or 4% of the estimated 379,881 vascular plant species worldwide (Paton et al., 2008) have been included in the list. Such low representation makes it difficult to use plant assessments as meaningful indicators of biological diversity. There is an increasing need for such measurable indicators in order for Red Lists to assess national and global targets for conservation and sustainability. The United Nations Environment Programme (UNEP) utilizes the IUCN Red List to measure progress toward its Millennium Development Goal 7, which is tasked to ensure environmental sustainability and thereby reduce biodiversity loss. Similarly, Target 12 of the Aichi Biodiversity Targets (2011–2020) of the Convention on Biological Diversity (CBD) also depends on conservation assessments, with the goal that by 2020 the extinction of known threatened species has been halted and their conservation status, particularly of those most in decline, has been improved and sustained (CBD, 2010a).

The Global Strategy for Plant Conservation (GSPC), which was adopted by Parties to the CBD in 2002, and revised in 2010 for a further 10 years (2011–2020), lays out a strategy for plant conservation. One of the 16 quantitative targets to be achieved by 2020 is Target 2: "[a]n assessment of the conservation status of all known plant species, as far as possible, to guide conservation action" (UNEP, CBD, 2010b; Wyse Jackson & Sharrock, 2011). To date, relatively few parties have made progress toward achieving this target (Secretariat of the CBD, 2009). A number of the other targets for the strategy depend on knowing which plants are threatened,

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especially Target 5, "[a]t least 75 per cent of the most important areas for plant diversity of each ecological region protected with effective management in place for conserving plants and their genetic diversity," Target 7, "[a]t least 75 per cent of known threatened species conserved in situ," and Target 8, "[a]t least 75 per cent of threatened plant species in ex-situ collections, preferably in the country of origin, and at least 20 per cent available for recovery and restoration programmes" (UNEP, CBD, 2010b, <http://www.cbd.int/gspc/targets.shtml>). Greater progress is needed in plant assessments in order to approach and to achieve the GSPC targets.

Between 2004 and 2008, South African botanists completed a comprehensive assessment of the status of the South African flora using the IUCN Red List categories and criteria (IUCN, 2001; Raimondo et al., 2009). South Africa is among 17 floristically megadiverse countries that collectively hold 70% of the world's species diversity (Mittermeier et al., 1997). South Africa is the first among these countries to comprehensively assess its vascular plant flora and to achieve Target 2 of the GSPC.

South African Plant Conservation

South Africa has the world's richest temperate flora, with 20,456 indigenous vascular plant taxa recorded (Raimondo et al., 2009). With the current global estimate of 379,881 taxa (Paton et al., 2008), 5% of the world's plant diversity lies within South African borders. In addition, the extraordinary level of vascular plant endemism, with ca. 13,265 taxa representing 65% of the flora, is singular and internationally recognized. South Africa is one of only two countries in the world that has three of the world's 34 biodiversity hotspots within its borders, namely the Cape Floristic Region (6210 endemics), the Succulent Karoo (2439 endemics), and the Maputaland-Pondoland-Albany Region (1900 endemics; Mittermeier et al., 2005). South Africa is indisputably a custodian of a significant store of the world's flora, both in terms of diversity and endemism. Monitoring the threat status of this extraordinary flora and ensuring its effective conservation is, therefore, a high priority.

South Africa has a centralized institution for biodiversity monitoring in The South African National Biodiversity Institute (SANBI), which is an independent entity linked to the Department of Environmental Affairs. SANBI is responsible for generating and disseminating information on the nation's biodiversity, and its findings are used to guide national conservation legislation and policy. As part of its mandate under the National Environmental Management: Biodiversity Act (NEMBA, 2004), SANBI must monitor and report on the conservation status of species and ecosystems. As a result, SANBI coordinates assessments of the conservation status of South African plant and animal species using the IUCN Red List categories and criteria. This builds on a long history of using the IUCN Red List system, where assessments of plant taxa date back to 1980 (Hall et al., 1980). Subsequent updates (Hilton-Taylor, 1996a, 1996b, 1997; Golding, 2002; Raimondo et al., 2009) have all utilized the IUCN Red List criteria of the time.

South Africa is fortunate among megadiverse countries to have a disproportionably high level of capacity in terms of taxonomic expertise and field botanists. The majority of the flora has received taxonomic treatment, with 62% of plant taxa having been revised since 1970 (Von Staden et al., 2013). In addition, a network of 20 local herbaria across the country house a representative sample of plant specimens, with the majority of specimens (90% of the country's ca. 3,263,200 plant specimens) concentrated in only six herbaria (BOL, GRA, NBG, NH, NU, PRE; National Research Foundation [NRF], 2011), three of which are managed by SANBI. Good electronic data in the form of digitized herbarium specimens and spatial layers for vegetation classification and national land use exist (Mucina & Rutherford, 2006), and 44% of South Africa's plant specimens have been electronically encoded (NRF, 2011). Most of these specimens are georeferenced to at least a quarter-degree square grid. This richness of taxonomic literature and electronic specimen and land-use data, combined with expert knowledge, enabled assessments to be carried out that satisfy the data requirements of the IUCN Red List categories and criteria.

Critical Success Factors

Critical success factors that allowed a large flora of over 20,000 plant taxa to be assessed within five years include a core team to coordinate and conduct Red List assessments, extensive collaboration with the local botanical conservation community, and the development of a data management system that serves local conservation needs.

ESTABLISH A RED LIST TEAM TO CONDUCT ASSESSMENTS

South Africa is one of a few countries with a team employed specifically to conduct IUCN Red List assessments. This team collaborated with an extensive network of 169 professional and amateur botanists from across the country to obtain information for plant

taxa. While conducting the threat assessments between 2004 and 2008, the team consisted on average of one project manager, three ecologists, and two support staff (e.g., student interns). A dedicated Red List team is considered essential for processing a large number of assessments as it reduces the need to train a large number of expert contributors in the use of the IUCN Red List system, which is complex and takes time to master. A small team of experienced staff can process a large number of assessments far faster than a large group of botanical experts dedicating their time toward threat assessments on a voluntary and part-time basis. The South African strategy delegated the core IUCN Red List team to host workshops and conduct interviews with taxonomic experts to efficiently obtain information not available in the literature or in electronic datasets. Although the IUCN Red List system is quantitative and objective, giving the responsibility of completing threat assessments to many different expert contributors results in inconsistent assessments, due to variation in precautionary and evidentiary approaches to listing among experts. A dedicated IUCN-trained team ensures consistency in the way the criteria are applied across different taxonomic groups. As with any large flora, at any given time there are many plant groups that are not receiving taxonomic attention, and, therefore, no botanical experts are available to do assessments for these groups. In such cases, the available botanical literature and taxonomic revisions need to be processed. Dedicated IUCN-trained Red List staff can focus on such plant groups. It is essential that scientists employed to do Red List assessments understand plant life histories and the response of plants to prevalent threats in different ecosystems. Field experience and a sound understanding of ecological characteristics of different habitats are also essential. IUCN Red List assessments are often undertaken by taxonomists, but in the South African experience, having a team of mostly ecologists working with taxonomists provided greater consistency in the interpretation of the environmental and biological parameters used to determine Red List status.

Although all South African assessments were done by SANBI Red List staff, it was absolutely vital to the success of the project that assessments were not done in isolation, and extensive collaboration with the local botanical conservation community was necessary. The Red List team acted as a central point through which the South African conservation community was involved in the listing process. The data informing the South African Red List were compiled with input from 169 professional botanists, taxonomists, conservationists, as well as amateur plant enthusiasts. These experts contributed a large volume of vital information not otherwise available in literature or spatial datasets. Whether or not the experts had extensive and recent field experience made the greatest difference to the value of the data they were able to contribute. Experts were consulted via workshops that focused either on plant families, particular plant groups, taxa of special interest (e.g., succulents, medicinal plants), or regional floras. Individual interviews were also held with experts throughout the duration of the assessment process. Collaboration with botanists based at local herbaria and academic and conservation institutes not only resulted in obtaining valuable IUCN Red List data, but also led to significant and widespread acceptance of the Red List as an important conservation tool. The IUCN Red List has subsequently been applied in many conservation initiatives, including the 2012 update of important legislation such as the list of Threatened and Protected Species on South Africa's Biodiversity Act (NEMBA, 2004).

STREAMLINE THE ASSESSMENT PROCESS VIA AUTOMATION

Electronically accessible herbarium specimens have been widely recognized as a useful resource whereby to conduct assessments of plant species (Schatz, 2002, 2009; Hernández & Navarro, 2007; Brummitt et al., 2008; Krupnick et al., 2009). Typically for countries with large floras, many plant taxa will be widespread and not threatened and the time spent assessing such common species should be minimized. In order to efficiently assess the large number of plant taxa that occur in South Africa, the assessment process was automated for widespread and common species. Electronic specimen data were used to automatically assign 9387 widespread taxa into the IUCN category of Least Concern (LC). Electronic specimen data were also used to prioritize 6000 taxa of restricted distributions that had never been assessed before, and these were targeted for further investigation. Based on this experience, the use of electronic specimen data is recommended as a first step in threat assessment to distinguish those species that are clearly widespread, abundant, and unlikely to be in danger of extinction from those species of lesser extent that need further investigation. This process focuses assessment resources on those plant species for which there is a greater likelihood that they could be threatened.

DEVELOP A DATA MANAGEMENT SYSTEM THAT SERVES LOCAL CONSERVATION NEEDS

When assessing a large number of species, a well-designed data management system can be a vital time-saving device. The IUCN promotes the use of

their Species Information Service (SIS) as a suitable data management portal for conducting assessments. This SIS system was developed at the same time that South Africa was assessing its flora, and one of the consequences is that South Africa developed its own relational database purposefully compatible with the SIS. Thus, we can compare the relative benefits of the IUCN SIS system from the time of the 2009 South African assessment with the local database in order to assess a large number of plant taxa from any area within the flora of a megadiverse region. The SIS system was developed to facilitate online assessment by IUCN specialist groups, where scientists working simultaneously on assessments may be based in a wide range of locations. In contrast, the South African assessments were conducted by a centralized team so the database did not need online capabilities and was constructed to interface with existing data sources in the country. For example, taxonomic information, such as scientific names, plant life history traits, and countries of occurrence, were automatically imported from South Africa's National Herbarium Computerized Information System (PRECIS), which saved significant time. Speed of data capture and ease of navigation are critical factors for allowing rapid completion of threat assessments. The SIS system allows for a large amount of data to be captured as part of the assessment process that may be relevant to species conservation but not necessarily critical in justifying categorization. Not only is completing the many data fields time consuming, but navigating through the associated forms can also significantly delay the completion of assessments. The South African approach was to select only a very limited number of critical data fields that could be displayed on a single form or screen view, and complete only those data fields for each species assessed, thereby allowing the completion of a large number of assessments within a short timeframe. SIS has recently made available the option to construct custom data views according to users' preferences and has improved ease of database navigation; however, allowing bulk data importing is still under review consideration.

The online SIS system constrains data held by the IUCN, such that this information is accessible only through IUCN-defined query protocols and is thus either not available or adaptable to answer novel and evolving local conservation questions. South Africa's threatened species database is more flexible, having been designed to serve local conservation needs, e.g., to provide the lists of species requiring protection from national and provincial conservation legislation as well as informing which species and even subpopulations to include as biodiversity targets in conservation plans.

The IUCN SIS is an international system, and, therefore, data capture options to support threat assessments are generalized and not adaptable to local data needs. In South Africa, not all data were captured as specified by the IUCN; instead, what was nationally required took precedence. For example, the IUCN's habitat classification system is too coarse for local requirements. Three of South Africa's nine major vegetation biomes comprise the Succulent Karoo, the Nama Karoo, and the Albany Thicket, which all fall under the IUCN's classification of Subtropical/Tropical Dry Shrublands. Data more locally appropriate for South Africa were captured, yet compatibility with SIS was maintained so that data could still be provided in the required format to the more globally relevant IUCN Red List.

Spatially georeferenced data for subpopulations of threatened species in South Africa turned out to be the single most useful dataset generated as part of the assessment process. It allowed for subpopulation distribution information to be intersected with other spatial information, such as vegetation maps or maps of protected areas, and this facilitated the automation of a large volume of the supporting data required by the IUCN. Other assessment projects for plants, including threat assessment of Madagascan and Hawaiian endemic plant families, have also relied heavily on georeferenced data (Schatz, 2002; Krupnick et al., 2009, respectively). In addition, spatial data associated with subpopulations is highly useful for informed conservation planning (Hoffman et al., 2008). The South African Red List database has been designed to capture spatial data associated with subpopulations. However, the IUCN SIS system does not currently have this capability.

Lessons Learned

(1) *Invest in using the IUCN system.* The latest version of the IUCN Red List categories and criteria is a quantitative, objective system that can be consistently applied across a range of taxonomic groups worldwide. The quantitative criteria are based on scientific studies of populations among many different species; these criteria also apply to the biological conditions under which they are highly likely to go extinct (Mace et al., 2008). The quantitative nature of the system demands that assessments be justified by supporting data that indicate how a species meets the conditions for inclusion in the threat category in which it is listed. This results in a high degree of transparency in the listing process. South Africa has found it valuable to

use the IUCN system because the Red List assessments for a number of species under threat have been legally challenged. This typically occurs when infrastructure, agriculture, or other developments are halted as part of the Environmental Impact Assessment process due to the presence of threatened species. The fact that the IUCN system is objective and scientifically based and is widely used internationally has meant that assessments for threatened plant species have been successfully defended. For example, a development that would have destroyed a subpopulation of the orchid *Brachycorythis conica* (Summerh.) Summerh. subsp. *transvaalensis* Summerh., an Endangered Red List taxon, was halted in 2011 in Gauteng Province, South Africa.

Further, the quantitative nature and transparency of the IUCN system enables more meaningful conservation decisions that are based not only on the threat category a species is listed under, but also on the different reasons a species may qualify as being in danger of extinction. In using the IUCN Red List, South African conservationists were able to consider how the threat criteria under which a species qualified could be used to recommend conservation actions or to set conservation targets. In conservation plans, for example, biodiversity targets for species vary by the threat category and also by criteria under which a species has been listed (Pfab et al., 2010). Similarly, guidelines dealing with threatened plant species in Environmental Impact Assessment reports are based not only on species status, but also on the qualifying criteria (Driver et al., 2009).

One of the perceived disadvantages of the IUCN system is that it is data intensive and, therefore, too time-consuming to complete large numbers of threat assessments for taxa within a reasonable time (Brummitt et al., 2008; Schatz, 2009). However, the quantitative and data-intensive nature of the IUCN Red List process was for South Africa one of its greatest advantages. The value of the data obtained as part of the threat assessment process for strategic, informed conservation decision-making outweighed the effort in capturing it. It became apparent that the problem with evaluating a plant species against the IUCN Red List criteria was not necessarily the amount of data required, but rather that resources were required to comply with the IUCN documentation requirements, i.e., the documentation required when an assessment is lodged with the IUCN. Many of the current documentation requirements for the IUCN have been developed to support analyses of the Red List database and are not necessary for reporting on the state of biodiversity at the international level, or for guiding conservation at the local level. South Africa has not submitted a full set of data for all species to IUCN, but instead has submitted only a minimum set of supporting data justifying the classification of plant species against threat criteria. A strict focus on a minimum set of supporting data is one of the main reasons it has been possible to assess 20,456 plant taxa within five years. The IUCN is currently reviewing the minimum data requirements partly on the basis of lessons learned from the South African plant assessment process.

Where the IUCN Red List system does not meet all local conservation needs, it is possible to augment it for national purposes without compromising its capability to be an effective international biodiversity monitoring tool. Because the IUCN system is focused entirely on determining a taxon's risk of extinction, it is less effective for prioritizing all taxa in need of conservation action. South Africa has a high number of range-restricted or rare endemics that are of high national conservation priority. However, if populations of such taxa are not declining, then the IUCN system would classify them with widespread and abundant taxa as Least Concern (LC). To address this, additional categories for highlighting taxa of conservation concern that were not detected by the IUCN system were developed for use in national conservation (Raimondo et al., 2009). For example, plant taxa known from only one subpopulation in South Africa but which face no threats were listed under the national category Critically Rare. Species that are listed according to this additional category appear on the South African national Red List but are classified as LC when the threat assessments are submitted to the IUCN Red List.

(2) *Quantitative assessments can be done with very little data.* Like many megadiverse countries, South Africa has many plant taxa that are poorly known. An estimated 38% or ca. 7000 taxa have outdated or no taxonomic treatment (Von Staden et al., 2013), and 26% or 5505 taxa have fewer than five specimens represented in the National Herbarium. Despite this lack of good data, it was possible to assign all South African plant taxa to one of the IUCN categories. Most assessments were desktop assessments done with only three basic information resources: taxonomic literature, electronic herbarium specimen data, and spatial land cover data. In South Africa, threatened plant species tend to be concentrated in specific areas where high levels of endemism coincide with high levels of threat, especially impacts of land use. Many plant species with similar distribution ranges and habitats are thus facing similar threats. Experienced assessors were able to

use their knowledge from assessing well-known species to infer the status of poorly known species from similar regions and habitats. Understanding the impact of local threats on particular life histories and ecological processes was central to this process. Because there is no monitoring data or recent field information available for most South African plant species, a civil society volunteer programme was established to gather information for the Red Listing process. This volunteer programme (the Custodians of Rare and Endangered Wildflowers) worked synergistically with the assessment process by prioritizing threatened, but poorly known species for field surveys (SANBI, 2012). Field data collected by volunteers were successfully used to either confirm the Red List status or to correct erroneous classifications of these previously poorly known species.

Brummitt et al. (2008) note that the majority of species listed on the IUCN Red List have been conducted by IUCN specialist groups with extensive field knowledge. They promote an approach to increase the number of plant taxa on the Red List, similar to that used in South Africa, in which non-experts conduct desktop assessments. Brummitt et al. (2008) specify that assessors need to have a thorough understanding of the IUCN categories and criteria, access to a database of georeferenced specimen collections, and some basic geography information system (GIS) knowledge. Our experience supports this approach as a practical way to assess large floras. However, a vital addition is that assessors need to have a sound understanding of the interactions between local threats and plant life histories and ecological processes in the region of assessment. In the South African assessment, this understanding was gained largely through extensive interaction of Red List staff with botanical experts, ably supplemented by the practical field experience of threatened plant surveys obtained through the Custodians of Rare and Endangered Wildflowers Programme.

(3) *Costs and cost-saving recommendations.* The South African Red List cost $593,291 to assess 20,456 taxa, at an average cost of $29 per taxon. This is relatively inexpensive when compared to other regional assessment projects. The Pan-Africa Freshwater Biodiversity Assessment that assessed 5000 taxa from a range of taxonomic groups cost $383.87 per taxon (W. Darwall, unpubl. data), whereas the European Red List, which assessed 5600 taxa also from varying taxonomic groups, cost $239 per taxon (M. Biltz, unpubl. data). Other estimates of the cost of conducting plant assessments have been as high as ca. $440 per taxon (Stuart et al., 2010), but the cost of the South African assessment was closer to the costs typically incurred when there is a large volunteer contribution. For example, the Global Cycad Conservation Status assessment, conducted by the IUCN Species Survival Commission (SSC) Cycad Specialist Group, cost ca. $26 per taxon (J. Donaldson, unpubl. data). In the case of the cycad assessment, the volunteer contribution has not been estimated, which emphasizes the low real cost associated with the South African Red List assessment. An assessment of selected plant families in Madagascar cost under $30 per taxon (Schatz, 2009). We thus predict that assessments of plants in other developing countries with megadiverse flora and fauna could also be done at a similar, reasonable cost. As megadiverse countries have high numbers of endemic plant taxa, it is worth the IUCN and conservation donors investing in supporting assessment projects in these countries in order to cost effectively increase the number of plant taxa on the IUCN Red List.

The approach adopted in South Africa meant that threat assessments of widespread and common species were automated, and only taxa that were of potential conservation concern were assessed in detail. In total, 12,044 South African plant species received focused attention. The cost of assessing these taxa of potential conservation concern decreased with time (Table 1), changing from $158.25 in the first year of assessment (2004) to $39.72 in the final year (2008). This change in cost was due to experience gained by assessors over the course of the project, which decreased the amount of time needed to assess each species. There is, therefore, a financial incentive to invest in a team of assessors when assessing a large number of taxa that may take several years to complete.

Consultation with experts was pivotal to the success of the South African Red List project and involved a combination of workshops and interviews. It was financially more efficient to assess species via interviews with individual experts than via workshops (Fig. 1), because in a large flora botanists tend to have specialized knowledge either of a certain region of the country or of a particular taxonomic group. As a result, there was little or no added value gained from bringing experts together, as expert knowledge seldom overlaps. However, some groups, such as medicinal plants, did require assessment via workshops because the impact of harvesting on populations needed to be debated with a range of the knowledgeable experts.

(4) *Comprehensive assessments ensure conservation attention for greater proportion of flora.* All previous Red Lists conducted in South Africa evaluated only a small proportion (less than 20%) of the indigenous

Table 1. Break down of staffing and costs of the South African Red List programme.

	2004	2005	2006	2007	2008
No. of support staff (e.g., student interns)		2	3		
No. of junior ecologists employed	1	3	5	1	1
No. of ecologists with over five years experience	1	2	1.5		1
Project manager	1	1	1	1	1
No. of expert consultants contracted	1		2	1.5	0.5
Total number of staff	4	8	12.5	3.5	3.5
Financial cost of staff	$80,506.33	$156,708.86	$206,075.95	$59,493.67	$76,708.86
Workshop expenses	$0	$3037.97	$2911.39	$1012.66	$1265.82
Expert interviews	$835.44	$278.48	$2227.85	$1392.41	$835.44
Total cost (U.S. $)	$81,341.77	$160,025.32	$211,215.19	$61,898.73	$78,810.13
No. of assessments conducted	514	3462	4537	1547	1984
Cost per assessment	$158.25	$46.22	$46.55	$40.01	$39.72
Total cost of project	$593,291.14				

flora. As a result of the first comprehensive assessment of all 20,456 taxa, 10% or 2045 taxa of conservation concern were added to the Red List for the first time. Of these, 942 were taxa threatened with extinction. The majority of these were historically of conservation concern but were never previously assessed (Fig. 2A). Many threatened taxa and other taxa of conservation concern are overlooked when only selective assessments are done. For example, one of South Africa's most threatened plant genera is *Marasmodes* DC. (Asteraceae). The six cryptic species in this genus were never all evaluated in a South African plant Red List before, even though they are all restricted historically to extensively transformed habitats and are all on the brink of extinction. The urgent conservation needs of the majority of the species in this genus were identified for the first time through this comprehensive assessment and resulted in an annual monitoring effort for the six described *Marasmodes* species as well as the discovery of four undescribed species. An argument often used against comprehensive threat assessments for plant conservation is that it is a waste of effort to try and assess all species when most are too poorly known to obtain enough data to measure against the criteria. Conducting a comprehensive assessment has allowed South Africa to identify the major gaps in botanical knowledge and has led to the prioritization of taxonomic research (Von Staden et al., 2013).

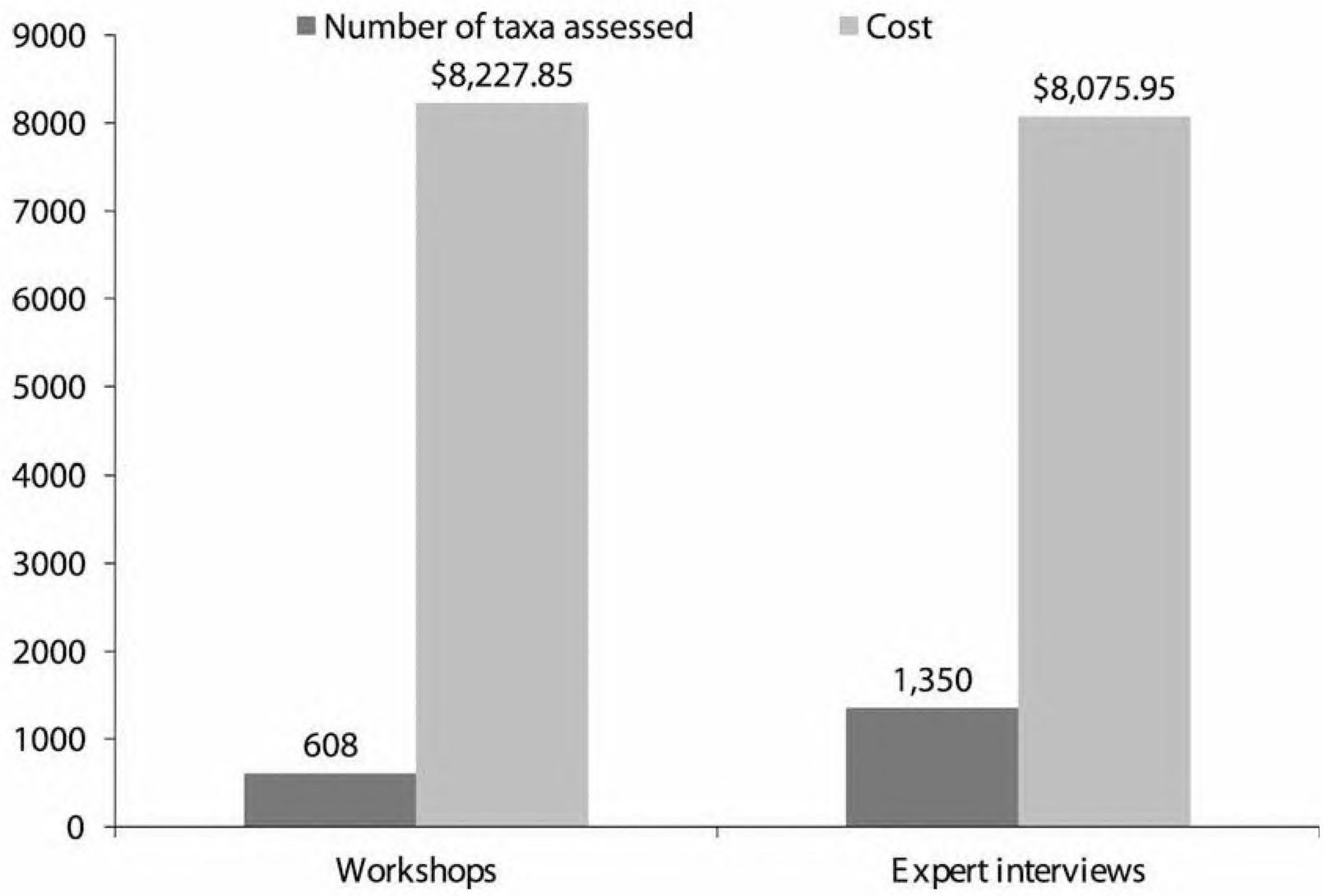


Figure 1. The total relative costs of conducting workshops or expert interviews are compared to the number of plant taxa assessed for South Africa via each of these approaches.

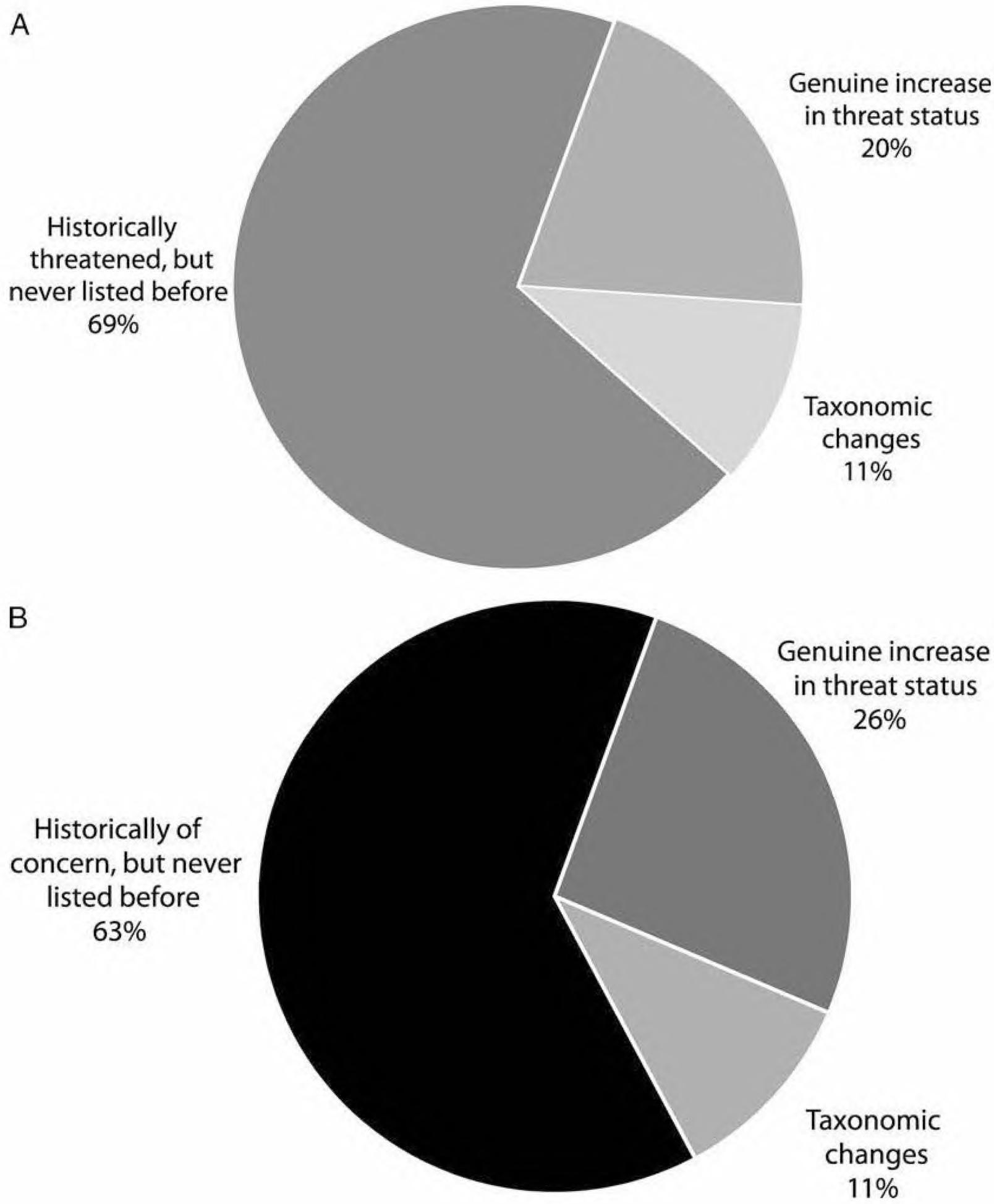


Figure 2. —A. Rationales for the addition of 942 taxa to categories of threat on the South African Red List for the first time. —B. Rationales behind the addition of 2045 taxa of any conservation concern to the South African Red List for the first time. Assessments follow the IUCN categories and criteria, version 3.1.

When comparing the proportion of threatened taxa in South Africa to those in other megadiverse countries, the impact of substantive assessment programmes becomes clear. South Africa, like other megadiverse countries that have conducted IUCN assessments of endemic taxa, has a high proportion (greater than 10%) of taxa that are threatened (Fig. 3). Other megadiverse countries such as Australia (20,148 plant taxa) and Brazil (35,107 plant taxa) that have not yet undertaken substantive assessment programmes have identified far lower proportions of their floras as threatened, only 4% and 6%, respectively (see Fig. 3) (Griffin & Hilton-Taylor, 2008; Chapman, 2009; Forzza et al., 2010, <http://floradobrasil.jbrj.gov.br>).

Conclusion

The South African experience shows that it is possible to assess a large group of plant taxa, such as the flora of a megadiverse country, using the global standard of the IUCN Red List system. The lessons learned from this process should inform the approaches adopted by other megadiverse countries as these will confer cost savings on similar projects and can help to make the Red Listing process more meaningful for local conservation action. Overall, the Red Listing process has had a positive impact on conservation efforts and is enabling South Africa to report against global targets for conservation and sustainability, such as those required by UNEP (Millennium Development Goals) and the CBD. As a

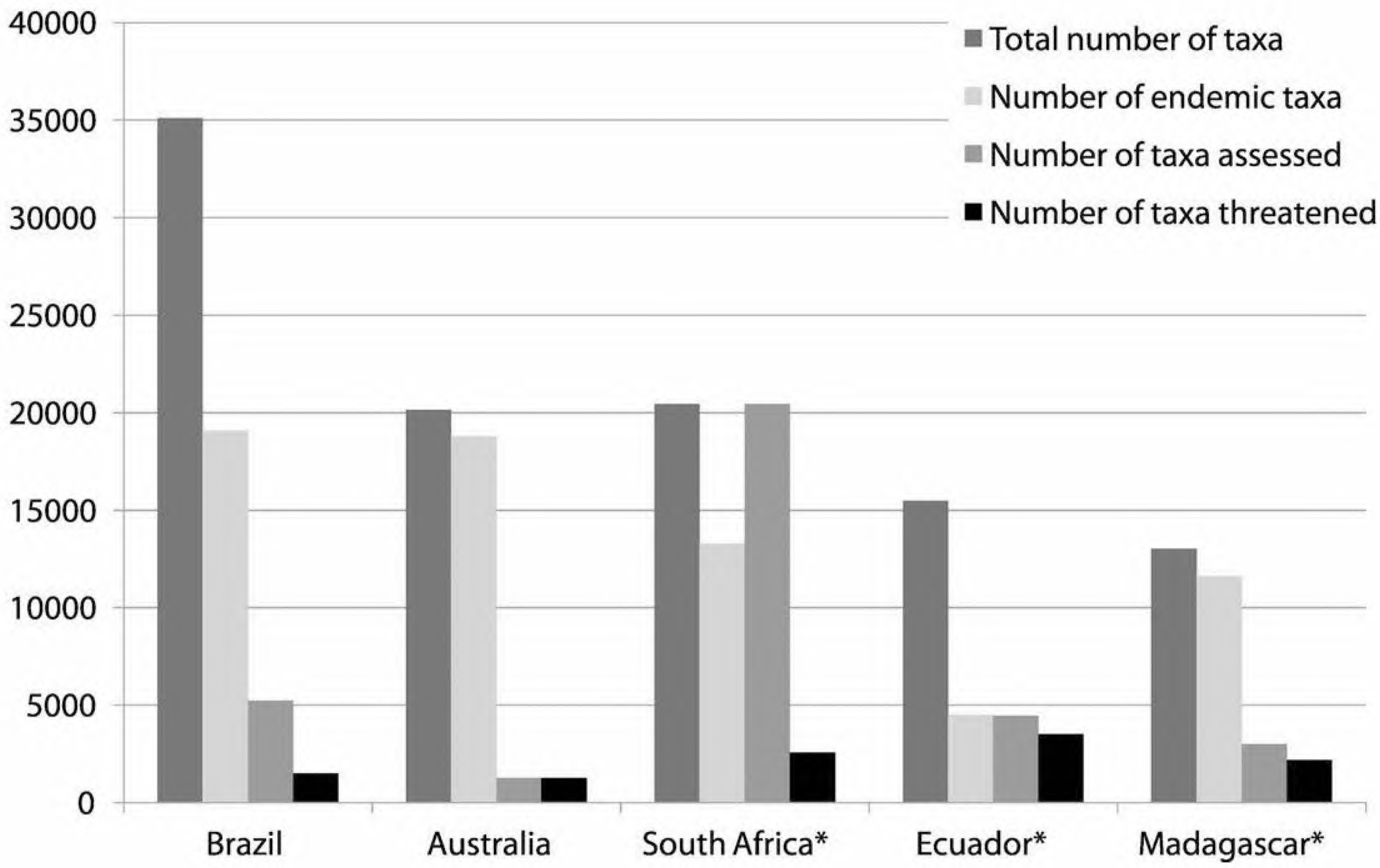


Figure 3. Taxonomic comparison of the five megadiverse countries: Brazil, Australia, South Africa, Ecuador, and Madagascar. Assessments in South Africa, Ecuador, and Madagascar (marked by asterisks, *) follow the IUCN categories and criteria, version 3.1. Data were obtained from Chapman, 2009 (Australia); Floradobrasil, 2010 (Brazil); Griffin & Hilton-Taylor, 2008 (IUCN); Groupes des spécialistes des Plantes de Madagascar (Madagascar); León-Yánez et al., 2010 (Ecuador); and Raimondo et al., 2009 (South Africa).

result, we encourage other megadiverse countries to conduct comprehensive conservation assessments, particularly of plants, using the IUCN system. As one step toward this goal, Red List training and experiences are currently being shared between Brazil, Colombia, and South Africa.

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A NETWORK APPROACH TO PLANT CONSERVATION IN NEW ZEALAND[1]

John Sawyer[2]

New Zealand has long been regarded as one of the world's biodiversity hotspots (Myers et al., 2000); therefore, the country's flora represents a global priority for plant conservation action. Factors influencing this significance are the high degree of endemism, the evolution of its species in a largely mammal-free environment dominated by birds, and the threatened status of its species and ecosystems. New Zealand has 60 endemic vascular plant genera, comprising 13% of New Zealand genera, and 1984 vascular plant taxa are endemic at the species and infraspecific level, representing 82.2% of these taxa (de Lange & Rolfe, 2010). In addition, 38% of New Zealand's indigenous vascular plants have been recognized as Threatened or At Risk (de Lange et al., 2009).

For the last two decades, plant conservation in New Zealand has been led by the New Zealand Department of Conservation (DOC; the central government agency charged with the protection of indigenous species) and local government (charged with environmental management under the Resource Management Act 1991), with participation from botanic gardens, nongovernmental organizations such as the Royal Forest and Bird Protection Society, the World-Wide Fund for Nature, as well as regional botanical societies. Numerous scientific institutions have researched New Zealand's flora, including most New Zealand universities and Crown Research Institutes (such as Landcare Research, National Institute of Water and Atmospheric Research, and AgResearch). From Sir Joseph Hooker's *Handbook of the New Zealand Flora* (1867) to Thomas Cheeseman's *Manual of the New Zealand Flora* (1906), there has been a long history of botanical research in New Zealand that culminated in the *Flora of New Zealand* nine-volume series (Allan, 1961; Moore & Edgar, 1970; Healy & Edgar, 1980; Galloway, 1985; Webb et al., 1988; Edgar & Connor, 2000; Galloway, 2007 [Vols. 1 and 2]; Engel & Glenny, 2008). All these organizations and agencies have demonstrated a strong desire to describe, understand, and protect New Zealand's unique plant life as part of a wider conservation movement that has existed in New Zealand for more than 100 years.

At the time New Zealand adopted the Global Strategy for Plant Conservation (GSPC) in 2002, there was limited coordination of national efforts, and no single agency appeared to be successfully championing the cause of New Zealand plant life. New Zealand needed a greater degree of coordination, advocacy, and action amongst the many governmental, nongovernmental, community, and research organizations involved in plant conservation in New Zealand.

Biodiversity Declines in New Zealand

The ongoing global decline in biodiversity has been documented widely and is caused by environmental changes such as climate change, habitat destruction, unsustainable harvesting, and the impact of invasive pests and naturalized plants (Butchart et al., 2010). In New Zealand, vascular plant populations and ecosystem structure and functioning are threatened by a broad suite of animal pests, including possums, rats, mice, mustelids (stoats, ferrets, weasels), goats, rabbits, pigs, deer, and stock. Bird and egg predation has impacted plant populations through loss of plant pollinators and seed dispersers (Anderson et al., 2011). Naturalized plants compete with native species; adventive species now outnumber native species in the wild (Howell & Sawyer, 2006). Humans continue to destroy intact indigenous plant communities and to intensify agricultural production in landscapes once dominated by indigenous plants. A lack of understanding of ecological declines has exacerbated the situation, with approximately 60% of New Zealanders believing the natural environment to be in good or very good condition (Hughey et al., 2008).

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This suite of environmental threats has conspired to increase the number of critically threatened vascular plant species by 60% over the last five years (de Lange et al., 2009). The most recent assessment of the conservation status of the flora occurred in 2009; 180 vascular plant taxa were listed as Threatened, which included 91 as Nationally Critical, 45 as Nationally Endangered, and 44 as Nationally Vulnerable, with an additional six taxa considered Extinct (de Lange et al., 2009). A further 651 plant taxa were listed as At Risk and comprise 83 Declining, six Recovering, 20 Relict, and 542 Naturally Uncommon taxa. In total, 38% of New Zealand's total indigenous vascular flora has been recognized as Threatened or At Risk (de Lange et al., 2009). Those declines precipitated a need for improved coordination to halt the decline in New Zealand's indigenous plants.

A Networked Approach, the New Zealand Plant Conservation Network

The New Zealand Plant Conservation Network (<http://www.nzpcn.org.nz/>) was formed in 2003 as a response to the GSPC (Convention on Biological Diversity [CBD], 2002) and the New Zealand Biodiversity Strategy as developed through the DOC and the Ministry for the Environment (MfE) in 2000. The New Zealand Plant Conservation Network came into being against a backdrop of a nationwide decline in native plants and was founded with support and advice from the Australian Network for Plant Conservation (<http://www.anbg.gov.au/anpc/>), which was established in 1991. The New Zealand Plant Conservation Network's vision is that: "No indigenous species of plant will become extinct nor be placed at risk of extinction as a result of human action or indifference, and that the rich, diverse and unique plant life of New Zealand will be recognised, cherished and restored." The New Zealand Plant Conservation Network is now composed of a collective of people and agencies reflecting all walks of New Zealand life (see Table 1). It is engaged in a wide variety of projects mostly stemming from the 16 targets of the GSPC including training, seed banking, research, and provision of information.

Table 1. Members of the New Zealand Plant Conservation Network, <http://www.nzpcn.org.nz>.

Botanic gardens
Plant nurseries
Researchers from New Zealand universities and Crown Research Institutes
Ecologists and land managers from central and local governments
Landowners
Gardeners
Botanists
Teachers
Business people

An Online Flora for New Zealand

The Network's first initiative in 2003 was the establishment of a web site to provide information about New Zealand's threatened vascular flora (<http://www.nzpcn.org.nz/page.asp?flora_vascular>). The overall Network web site (<http://www.nzpcn.org.nz>) has since grown to become a central repository for information about New Zealand's flora including all native and naturalized vascular plants, liverworts, mosses, and some fungi. It is now the central hub for the New Zealand Plant Conservation Network in all its communications and is used by Network members to communicate with each other using the online forum, to learn about plants and ecosystems, to buy publications, to test their knowledge of the flora using an online quiz, to read the news or newsletters, and to download species factsheets and plant photographs. The web site now receives more than 450,000 visits annually (cf. Table 2). Site visitors can download species information as PDF files automatically created by harvesting information from online databases or can make personalized plant books of up to 20 species. The web site provides links to other botanical resources such as New Zealand herbaria, the New Zealand digitized flora (<http://floraseries.landcareresearch.co.nz/pages/Index.aspx>), and plant nursery web sites.

Online Phenology Recording in New Zealand

A phenology recording system was built in 2010 and installed on the New Zealand Plant Conservation Network web site to allow recording of observations of plant flowering, fruiting, and dieback. This feature was intended to complement other international initiatives such as Project Budburst in the United States. (<http://neoninc.org/budburst>) and Nature Detectives in the United Kingdom (<http://www.naturedetectives.org.uk>). Both provide citizen scientists with a tool to document local changes in phenological events over time and to compare regional results with those from other parts of their respective country and with historically documented flowering and fruiting times. This also provides plant nurseries and community groups and landowners involved in ecological restoration with valuable real-time information about regional seed collection times.

Table 2. Features and usages of the New Zealand Plant Conservation Network online, <http://www.nzpcn.org.nz>. The web site receives more than 450,000 visits annually.

Features	Daily Usage
More than 23,000 plant photographs	1200 site visits per day
6500 species pages	800 documents downloaded daily (average over six months)
Links to other botanical resources	20,000 images viewed daily (average over six months)
Online quiz	
Make your own book system	
Species factsheet PDF maker	

Since June 2010, more than 8000 phenology records have been made to the New Zealand Plant Conservation Network's phenology recording system.

Plant Advocacy and Public Outreach in New Zealand

Raising public awareness of native plants is a high priority for the New Zealand Plant Conservation Network to prevent further declines in indigenous plant populations and ecosystems. The focus for this advocacy has been to raise awareness of the threats that plants face in the wild and of the actions people can take to sustainably use and conserve vascular plant taxa. This has been achieved through a variety of means (cf. Table 3). An annual award scheme was started in 2005 and is used to identify people and organizations that have made the greatest contribution to plant conservation in New Zealand. Awards have been made to schools, plant nurseries, individuals, local government, and communities. An annual vote to find New Zealand's favorite plant was begun in 2002 by Professor Ian Spellerberg (Lincoln University, New Zealand). The purpose was to discover why New Zealanders love their native plants and to promote the flora. Since 2005, this vote has been conducted via an online voting system on the New Zealand Plant Conservation Network web site. Winners have included: *Lepidium oleraceum* G. Forst. (2005, Cook's scurvy grass, Brassicaceae); *Brachyglottis huntii* (F. Muell.) B. Nord. (2006, Chatham Island Christmas tree, Asteraceae); *Epilobium microphyllum* A. Rich. (2007, willowherb, Onagraceae); *Ficinia spiralis* (A. Rich.) Muasya & de Lange (2009, pingao, Cyperaceae); and *Myosotidium hortensia* (Decne.) Baill. (2010, Chatham Island forget-me-not, Boraginaceae). The New Zealand Plant Conservation Network has published numerous books, reports, and materials that promote plants and include a monthly newsletter (*Trilepidea*), a threatened plant poster, national plant checklists for native and naturalized species (cf. Howell & Sawyer, 2006; de Lange & Rolfe, 2010), and a detailed assessment of the threatened plants of New Zealand (de Lange et al., 2010). These publications are sold via an online shop on the Network's web site (<http://www.nzpcn.org.nz/shop_products.asp>).

Table 3. Advocacy by the New Zealand Conservation Network.

Annual awards scheme
Vote for your favorite plant competition
Publications, including newsletters, promotional materials, plant checklists and books
Submissions on government policy

Plant Conservation through Marae-based Training

To increase plant conservation capacity and capability, the New Zealand Plant Conservation Network has developed a plant training course consisting of four modules. Each module is designed for delivery over a two-day period on a marae (a traditional Maori tribal meeting place). Those modules are: (1) an introduction to plant life in New Zealand (Reid et al., 2009); (2) managing conservation covenants (Reid & Sawyer, 2010); (3) native plant nursery management and plant cultivation (Reid et al., 2011); and (4) streamside and wetland management (Singers & Reid, in prep.) These modules are intended to provide a marae-based learning experience, to increase plant identification, pest control, and plant propagation skills, and to expose an increasing number of people to plant conservation principles and techniques.

Ex situ Conservation in New Zealand

The New Zealand Plant Conservation Network developed the New Zealand Threatened Plant Seed Bank (<http://www.nzpcn.org.nz/page.asp?conservation_seedbank>) as a contribution to the global initiative run by Kew's Millennium Seed Bank affiliated with the Royal Botanic Gardens, Kew, in the United Kingdom (<http://www.kew.org/science-conservation/save-seed-prosper/millennium-seed-bank/index.htm>). Seed bank-

ing was identified as a high priority by the Network due to the earthquake-prone nature of the New Zealand landscape. Ex situ insurance populations would be especially significant should wild plant populations be destroyed. Ex situ seed banking was also seen as a relatively cheap way to protect indigenous plants. This work was sponsored by MWH-New Zealand Ltd. (a private engineering and environment company). The seed bank itself was established at the Margot Forde Germplasm Centre in Palmerston North and is managed by AgResearch (<http://www.agresearch.co.nz>), which was originally set up to store agricultural seed.

David Given Threatened Plant Research Trust

In 2007, the Network established the David Given Threatened Plant Research Trust in memory of David Given, who contributed significantly to plant conservation in New Zealand and globally. Given's work in New Zealand was an important building block of the current threatened plant program, including threatened plant listing and advocacy (see Given, 1976, 1981). The trust was established to provide regular scholarships to researchers studying threatened plants and plant communities in New Zealand.

Challenges in New Zealand toward the GSPC 2020 Goals

The New Zealand Plant Conservation Network is a hugely successful product of the GSPC (CBD, 2002). By providing a local, in-country response to the global plant conservation crisis, the New Zealand Network has shown what can be achieved by harnessing the power of individuals and organizations to achieve a common purpose. Despite the notable successes of this national plant network, a number of challenges remain for plant conservation in New Zealand. These can be categorized into four themes, as follow.

(1) In-situ protection of critically threatened species populations. Nature conservation resourcing is not always aligned strongly with the needs of New Zealand's most threatened plant species and ecosystems. Limited funding exists to resource threatened plant species or ecosystems. Many funds support common, more charismatic plant species and ecosystems as a preference. There is no legislation protecting threatened plant species in the wild, irrespective of land tenure. Securing greater funding for threatened species and ecosystems is a New Zealand Plant Conservation Network priority to target active management of important plant areas.

(2) Education and advocacy. Increased public awareness is needed of the role that plants can play in fixing environmental problems. Many challenges facing land managers can be ameliorated through the use of plants. Plants may be used to improve flood prevention, soil conservation, carbon sequestration, coastal and riparian infrastructure protection, and provision of shade and shelter to humans. Advocacy about these roles of plants and the way humans can make use of them will increase the value they attribute to them in the landscape.

(3) Use and appreciation of plants. A key ingredient in the decline in native plants in New Zealand is their invisibility. A critical job is to position native plants at the heart of landscapes, cities, and, therefore, human consciousness. The integration of plant conservation into the management of economically productive land is also a challenge facing New Zealand. A historic dichotomous view of land use has evolved, whereby native species are confined to parks and reserves, and economic production occurs in the areas between which are largely free of native species.

(4) Capacity building. A priority for the New Zealand Plant Conservation Network is to build the Network's training modules into a national Diploma in Plant Conservation to increase the number of people with plant conservation skills. Another challenge is to increase the size of the David Given Threatened Plant Research Trust fund to provide more frequent and larger scholarships. The future expansion of the New Zealand Plant Conservation Network's program to become a partner in a Pacific-wide organization may also be considered. Such an organization could provide opportunities for technology and skill transfer throughout Oceania or the Pacific Oceanic Islands. This may include monitoring, seed banking, propagation, information management, pest control, and habitat protection in places where indigenous plants face similar threats as seen in New Zealand.

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TOWARD THE IMPLEMENTATION OF GLOBAL STRATEGY FOR PLANT CONSERVATION TARGETS 1 TO 3 IN HAWAI'I[1]

Chipper Wichman[2] *and Margaret Clark*[2]

ABSTRACT

Hawai'i has a unique natural history, ideal for studying the mechanisms of evolution. With over 90% endemism in its native flora of 1300 species, over half are threatened with extinction. This immense challenge requires working collaboratively, effectively, and efficiently. Despite extensive conservation activity, we do not have a unified strategy, and leaders in Hawaiian conservation are discussing the creation of a Hawai'i Strategy for Plant Conservation (HSPC) based on the Global Strategy for Plant Conservation (GSPC) targets. Here we analyze the effectiveness of the conservation work taking place in Hawai'i through the lens of the GSPC Targets 1 to 3 that include: (1) the establishment of an online flora of all known plants; (2) the assessment of the conservation status of all known plant species; and (3) the development and sharing of research and methodology related to on-the-ground conservation.

Key words: Biodiversity, endemism, extinction, Global Strategy for Plant Conservation (GSPC), Hawai'i Conservation Alliance (HCA), Hawai'i Rare Plant Restoration Group (HRPRG), Hawaiian flora, IUCN, U.S. Fish and Wildlife Service (USFWS).

The framework of the international Global Strategy for Plant Conservation (GSPC) is an effective way to tie Hawai'i's conservation programs together and to measure progress toward those updated GSPC goals established at the 10th meeting of the Conference of the Parties to the Convention on Biological Diversity, 18–29 October 2010. As concluded in Nagoya, Japan, Objective I of the GSPC stated that plant diversity is well understood, documented, and recognized. Under Objective I, the GSPC uses three targets that are designed to measure the effective implementation of this objective. Target 1 is an online database for the flora; Target 2 documents the conservation status of the flora; and Target 3 refers to the dissemination and sharing of information.

Hawai'i is an ideal place to study plant evolution, because its biodiversity developed in the extreme isolation of the mid-Pacific without human interference. The Hawaiian archipelago arose from the central Pacific Ocean floor as a sort of conveyor belt of volcanic activity, emerging from the southeast, moving toward the northwest, beginning some 70 million years ago. From 230 plant colonizations, it is estimated that the archipelago evolved approximately 1345 endemic species of flowering plants (Wagner et al., 1999) and ferns (Palmer, 2003). The steep volcanic topography of the islands, with many narrow mountain drainages and inaccessible habitats, provided many small ecological niches. Taxonomic radiation into these niches led to an extremely high degree of endemism. Ninety-four percent of all dicot species are estimated to be endemic to the archipelago (Wagner et al., 1999) and a large number of those are single-island endemics, often restricted to one valley. Since human colonization only occurred an estimated 1000 to 1200 years ago, and there are no native land mammals apart from one bat species, threats to this flora were, until recently, relatively insignificant.

This contrasts dramatically to the "post-contact" competition from new introductions, be these human, animal, plant, insect pest, or disease. Over half of the remaining endemic flora is now considered at risk of extinction. With an extraordinary assemblage of more than 28,000 native plants and animals, as catalogued by the Hawaii Biological Survey database (<http://hbs.bishopmuseum.org/hbsdb.html>), the Hawaiian archipelago is one of the world's most ecologically diverse locations. A large percentage of these taxa are endemic (cf. Fig. 1). The vulnerability of these unique natural resources makes Hawai'i a microcosm for the practice and science of global bio-cultural conservation, which should be measured through an international framework like the GSPC.

This immense natural challenge requires working collaboratively, effectively, and efficiently. Despite

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Figure 1. Endemic Hawaiian plants under threat. —A. *Lobelia gloria-montis* Rock, pu‘u kukui or bog lobelia (Campanulaceae). —B. *Scaevola glabra* Hook. & Arn., ohe naupaka or camphusia (Goodeniaceae). —C. *Lysimachia daphnoides* Hillebr., lehua makanoe (Primulaceae). —D. *Polyscias bisattenuata* (Sherff) Lowry & G. M. Plunkett [≡ *Tetraplasandra bisattentuata* Sherff], ohe ohe (Araliaceae). Photos taken by Ken Wood, National Tropical Botanical Garden.

extensive conservation activity, we do not have a unified strategy, and leaders in Hawaiian conservation have discussed the creation of a Hawai'i Strategy for Plant Conservation (HSPC) based on the GSPC targets. An HSPC modeled after the GSPC will focus attention and resources on Hawai'i more effectively than the North American Botanic Garden Strategy for Plant Conservation (<http://www.bgci.org/files/Worldwide/Conservation/north_american_plant_conservation_strategy.pdf>), due to Hawai'i's unique location and natural history. The North American strategy was not written to include Hawai'i, presumably because of the dissimilarity of both the flora and the geography. The following attempts to analyze the effectiveness of the conservation work taking place in Hawai'i through the lens of GSPC Targets 1 to 3. It is important to update the national and international conservation communities on the status of the unique flora that has evolved in this biodiversity hotspot, because while the Hawaiian Islands have been visited by botanists for over 200 years, there have also been many contemporary initiatives by numerous organizations to conserve the native flora.

Target 1, an online database for the flora, has been accomplished, and Hawai'i currently has very good online documentation of its flora. Classification and naming of the Hawaiian flora began with indigenous Hawaiian culture over 1000 years ago. Western documentation based on the Linnaean system (binomial) was begun over 200 years ago, with the arrival of the Europeans. Botanists traveling with early explorers like Captain James Cook (three voyages, 1768–1779) and George Vancouver (1792) made the first known botanical collections and drawings of the Hawaiian flora. Approximately a century later, the first *Flora of the Hawaiian Island* was published by a German physician living in Honolulu (Hillebrand, 1888). Since western botanists began their investigation of the Hawaiian flora, over 100 species have gone extinct. At the same time, due to the rugged nature of the islands, dozens of new species are still being discovered. Since the flora was last systematically revised in 1990, the National Tropical Botanical Garden's (NTBG) field botanists have discovered 45 new species and a further 35 species thought to be extinct, which has expanded the existing flora by a total of 65 species (Wood, 2011).

The publication of the *Manual of Flowering Plants of Hawai'i* by Wagner et al. (1999) was a landmark effort to document the flora using modern systematic methods and remains the reference publication for all botanical research in the Hawaiian Islands, in spite of the fact that taxonomic revisions since its publication have been considerable. A parallel reference for the pteridophytes is *Hawai'i's Ferns and Fern Allies* by Palmer (2003). In collaboration with the NTBG, the Smithsonian Institution (SI) maintains an online version of the *Flora of Hawaiian Islands* (Wagner et al., 2005), which is updated with periodic supplements (<http://botany.si.edu/pacificislandbiodiversity/hawaiianflora/Hawaiian_vascular_plant_updates_1.3.pdf>).

In addition to this online flora, a number of other online resources are available. Collaboration between the Royal Botanic Gardens, Kew, and Missouri Botanical Garden (MO) created an online plant names index (<http://www.theplantlist.org>), which includes Hawaiian species. The Plant List combines multiple checklist data sets held by those institutions and other collaborators, providing the accepted Latin name for most species, with links to all synonymous names by which the taxon has been known.

Extensive collections of plant specimens are deposited in the herbarium at the Bernice P. Bishop Museum in Honolulu (BISH; <http://www2.bishopmuseum.org/HBS/checklist/query.asp?grp=Plant>). A geographical search engine is available through the MO Tropicos database (<http://www.tropicos.org/SpecimenGeoSearch.aspx>) and through the herbarium of the NTBG (<http://ntbg.org/herbarium>). The two Hawaiian herbaria, BISH and PTBG, as well as those at SI, New York Botanical Garden (NY), and MO, extensively document Hawaiian and other Pacific flora. The PTBG's type collections have been digitized and made available online on JSTOR Plants as the result of funding from The Mellon Foundation. Another project, the Consortium for Pacific Herbaria (CPH) funded by the U.S. National Science Foundation, is in progress to database and digitize Hawaiian and Pacific Island herbaria and make them available online through a single web portal hosted by the University of Hawai'i (<http://www.herbarium.hawaii.edu/cph/index.html>).

Other particular lists for the Hawaiian flora or locales corroborate the larger online databases and herbarium collections. These include a checklist of Native and Naturalized Flowering Plants of Hawaii, including the islands of Oahu, Hawai'i, Maui, Molokai, Lana'i, Kaho'olawe, Kaua'i, and Ni'ihau (<http://www.bishopmuseum.org/research/natsci/botany/dbandkeys/Main%20Islands%20Report.pdf>). Another checklist documents the northwestern Hawaiian Islands of Nihoa, Necker, French Frigate Shoals, Gardner Pinnacles, Maro Reef, Laysan, Lisianski, Pearl and Hermes Atoll, Midway, and Kure Islands (<http://www.bishopmuseum.org/research/natsci/botany/

dbandkeys/NWHI%20Islands%20Report.pdf>). Other national databases include Hawaiian plants and can be found through the Botanic Gardens Conservation International (BGCI; <http://www.bgci.org/plant_search.php/>), The Center for Plant Conservation (CPC; <http://www.centerforplantconservation.org/collection/NationalCollection.asp>), and NatureServe (2011; <http://www.natureserve.org/explorer/>). These databases incorporate data from the Hawai'i Biodiversity Mapping Program. In addition, several other databases maintained by the University of Hawai'i contain excellent photographic archives of Hawai'i's flora. The Hawaiian Native Plant Genera database (<http://www.botany.hawaii.edu/faculty/carr/natives.htm>) includes photographs of dicots, monocots, ferns, and fern allies, arranged by family and genus, and to the species level. The Plants of Hawai'i database contains both native and introduced species as well as indigenous plants (<http://www.hear.org/starr/images/?o=plants>).

Target 2 of the three GSPC targets focuses on the assessment of the conservation status of all known plant species, as far as possible. The U.S. Fish and Wildlife Service (USFWS) has the most complete data on the current status of Hawai'i's flora. Of all federal listed plants in the United States (760; <http://ecos.fws.gov/tess_public/pub/Boxscore.do>), almost half (357) are Hawaiian taxa (<http://ecos.fws.gov/tess_public/pub/stateListingAndOccurrenceIndividual.jsp?state=HI&s8fid=112761032792&s8fid=112762573902>). With current taxonomic changes, the number of federally listed Hawaiian plant taxa is 370. USFWS estimates that at least half of those taxa are limited to fewer than 1000 individuals each (Table 1).

Under the Endangered Species Act, taxa designated as Threatened (T) or Endangered (E) or candidates for listing are listed in the USFWS's Environmental Online Conservation System, either alphabetically by scientific name at <http://ecos.fws.gov/tess_public/pub/listedPlants.jsp> or alphabetically by common name at <http://ecos.fws.gov/tess_public/pub/stateListingIndividual.jsp?state=HI&status=listed>. On each species page on the USFWS web site, species profile pages for assessed species contain links to documents, including the initial proposed listings, recovery plans, critical habitat designations, and five-year reviews. These describe the conservation status of an individual species, any relevant taxonomic changes, life history research, associated habitats and species, as well as any threat to its survival. Conservation measures are recommended and implemented for species recovery. Five-year reviews have recently been completed for all Hawaiian threatened and endangered plants, with the exception of those most recently listed in 2010. Although not exhaustive, this is the best single source for information on the conservation status of Hawai'i's rare plants. It is estimated that another 78 Hawaiian plant species will be listed in the next few years (USFWS, 2012a, 2012b, 2012c), according to a new USFWS work plan available at <http://www.fws.gov/endangered/improving_ESA/listing_workplan.html>.

Table 1. U.S. Fish and Wildlife Service (USFWS) population data on the Hawaiian flora.

Abundance	# of taxa
Extinct	115
In captivity only	19
1 in the wild	12
2–20 in wild	95
21–100 in wild	123
101–1000 in wild	205
1001–5000	83
> 5000 in wild	637
Unknown	56
Total	1345

Data taken from USFWS (2011). Taxonomic note: USFWS has listed some entire species, which include a number of subspecies, and in other species only some subspecies. Subsequent to listing some taxonomic revisions have resulted in the listed species being split into a number of new species.

Another 260 Hawaiian plant species are informally designated as species of concern in the USFWS. Species of concern is an informal term not defined in the federal Endangered Species Act, but it commonly refers to species that are declining or may be in need of conservation. Species of concern may be identified as those with some or all of the following indicators:

(1) Magnitude of decline. For the species of concern, the recent rate of decline is compared relative to the historical extent of decline.

(2) Natural rarity. The plant species of concern is known only from a small number of specimens or occurs infrequently and in small numbers because of ecological or evolutionary factors.

(3) Restricted endemism. The species of concern is native to a particular and limited geographical range and is found only there.

(4) Connectivity of populations. The level of possible reproductive exchange among populations of the species of concern is estimated, given the number and distribution of known populations.

(5) Habitat. The species of concern has unique or highly specific habitat requirements that support careful monitoring of its status.

With such species of concern added to those that are officially listed, over 50% of the Hawai'i flora is considered to be at risk.

Two hundred three species with less than 50 individuals seen in the wild have been identified under the Plant Extinction Prevention Program of Hawai'i (PEP) for priority recovery efforts (<http://pepphi.org/>). The PEP list includes 49 species that are not already listed by USFWS. These additional species are also tracked in a Statewide Rare Plant Database, with regular updates from PEP field botanists on each island.

An earlier version of a statewide database, the Heritage Database, now called the Hawai'i Biodiversity Mapping Program database, contains all the historical occurrences of listed species, but has only been updated through about 2002, due to lack of resources. Additionally, the U.S. Army, Oahu, maintains its own database on those 66 Hawaiian species federally listed as T or E for which it is responsible (U.S. Army, Center for the Environmental Management of Military Lands, Colorado State University; U.S. Army, Oahu Army Natural Resource Program, U.S. Army Garrison Hawaii and Pacific Cooperative Studies Unit, 2010). Regular annual status reports on the conservation status and recovery of these species are available online at <http://manoa.hawaii.edu/hpicesu/dpw_mit.htm>.

Unfortunately, the International Union for Conservation of Nature (IUCN, 2001) Red List, which is considered the international standard for threatened and endangered species, includes only 224 endemic and two indigenous species from Hawai'i (<http://www.iucnredlist.org/>). This is in contrast to the higher number of species federally listed as T and E or on the PEP list. It is interesting that the Red List actually included several species as Vulnerable (VU) that are not listed as rare by either the state of Hawai'i or the USFWS. The Hawai'i Rare Plant Restoration Group (HRPRG), IUCN's Specialist Group for Hawai'i, has requested help in completing the IUCN listing process for additional species but has had no funding for the purpose, and the listings remain incomplete at this time. Until all T and E, PEP, candidate, and species of concern species are listed under IUCN, the global significance of the taxonomic endangerment, indeed extinctions, of the Hawaiian flora is not reflected accurately under the IUCN Red List.

A number of studies have been conducted documenting the diverse plant communities and their distribution in Hawai'i. The composition of Hawai'i's coastal plant communities has been well documented by Warshauer et al. (2009). Another project in 2007 mapped distributional ranges for four plant species, two widespread and two rare, on all the main Hawaiian Islands (Price et al., 2007), and Hawai'i was one of a number of island archipelagos reviewed for conservation priorities by Caujapé-Castells et al. (2010). This last article, however, used the IUCN listings for its statistics on rare plants in Hawai'i, so it provides an underestimate and does not reflect the actual gravity of the extinction crisis in Hawai'i's endemic flora.

The NTBG has over three decades of collection data in both its Living Collections Database and Herbarium Database (<http://www.ntbg.org/herbarium/>). In addition, the Plant Recovery Coordinator for USFWS-Honolulu maintains a database that includes candidate species not yet listed, and species of concern that are assessed to need evaluation as possible candidates for federal listing. Information is maintained on the known status of numbers of populations, individuals, threats, and latest observations. The conservation status of rare plants requires regular monitoring and updating, and more field botanists are needed to collect this information. Staffing also limits IUCN Red listing assessments for many species, so the actual endangerment of the Hawaiian flora is not accurately reflected internationally.

Target 3 of the GSPC is that information, research and associated outputs, as well as the methods necessary to implement the strategy are developed and shared. This has been implemented in many significant directions, but not in the context of the GSPC. Our recommendation is that the conservation and research community establish a mechanism, perhaps through the Hawai'i Conservation Alliance (HCA), that will effectively compile and index progress toward implementing the GSPC targets.

In general, research and conservation efforts in Hawai'i have been collaborative and various groups regularly share information with each other. Perhaps this is because everyone recognizes the magnitude of the problem and agrees that we are working toward a common goal and will need to work together if we are to achieve our goals. One way in which this collaboration has expressed itself is via the HCA, an organization of 19 leading federal and state agencies and NGOs that meet regularly to discuss conservation issues and share information. This target is being met by a wide variety of collaborative projects, database coordination, sharing of on-the-ground restoration techniques, and scientific research, but more science in support of conservation efforts is cogently needed.

The HCA has clearly noted the need for increased research that will inform effective conservation in Hawai'i (<http://hawaiiconservation.org/files/content/activities/effective_conservation/

effectiveconservationoverview.pdf>). Although science in support of conservation has been extensive over the past several decades, the sheer size of the endangered flora dictates that much more needs to be understood about Hawaiian species. More genetic analysis, pollination biology, life history and phenology, soil ecology, and related studies are needed for conservationists to effectively assess and conserve the at-risk species. Very few genera are well characterized across these disciplines, let alone the numerous species that represent Hawai'i's plant diversity. We still have much to learn in understanding how sympatric speciation, obligate outcrossing, co-evolution, indeed any species interaction, may impact any species' ability to regenerate and maintain themselves in the face of changing ecosystems. Understanding both internal and external reproductive barriers and how they evolved is also essential to long-term management of rare species.

While climate change has now been recognized as an official threat to rare species by the USFWS, the research on what this will mean in Hawai'i is just beginning. The Pacific Islands Climate Change Cooperative (PICCC; <http://piccc.net>) is a new interagency organization whose purpose is to assist those who manage native species, island ecosystems, and cultural resources in adapting their management to climate change in the Pacific Islands. PICCC coordinates the important research that needs to be done so that appropriate mitigation strategies can be developed. While the need for more research has been identified, a lot of information has already been accumulated and more is being acquired every year. Several key advances have been made to share this information among the members of the conservation and research communities.

Sharing the Science

The HCA (<http://hawaiiconservation.org>) is a coalition of 19 conservation organizations working together to protect and restore the natural resources of Hawai'i. A list of its institutional members (<http://hawaiiconservation.org/about/alliance_partners>) demonstrates the breadth and depth of cooperative commitment that has been made. Coordinated by the HCA, the Hawai'i Conservation Conference (HCC) is an annual three-day conference and is the largest conservation gathering in Hawai'i. Typically attended by ca. 1000 participants, the HCC has become an effective venue that facilitates sharing research results through forums, symposiums, workshops, lectures, and other media (<http://hawaiiconservation.org/activities/hawaii_conservation_conference>). An annual Nahelehele Dryland Forest Symposium is sponsored by Ka'ahahui O Ka Nahelehele (<http://drylandforest.org>), a Hawai'i island nonprofit organization. Its participating organizations and projects can be found at <http://drylandforest.org/partners>. In May 2011, SI and NTBG, with support from other organizations, co-sponsored a three-day scientific conference, "Evolution of Life on Pacific Islands and Reefs: Past, Present, and Future," in Honolulu. The conference proceedings are available at <http://botany.si.edu/events/2011_pacific>.

The Hawaiian Ecosystems At Risk (HEAR) website (<http://www.hear.org>) maintains a number of databases, image collections, and listservers that share technology, methods, and information in order to facilitate communication among decision-makers, resource managers, and the general public in support of effective science-based management of harmful non-native species in Hawai'i and the Pacific. HEAR also provides online discussion forums for a large number of conservation specialist groups, including all invasive species councils, environmental educators, and specialist groups on invasive plant pests and others (<http://www.hear.org/hearlists/index.html>).

The University of Hawai'i hosts a number of important conservation research facilities including the Center for Conservation Research and Training (<http://www.hawaii.edu/ccrt/CCRTOnline/Programs.html>). Other resources include the Hawai'i Seed Research facility at Lyon Arboretum, the Hawai'i Stream Research Center, and the Ecology, Evolution, and Conservation Biology Graduate Program. The University of Hawai'i Department of Botany also hosts the Hawaiian Plant DNA Library (<http://www.botany.hawaii.edu/faculty/morden/HPDL.htm>), the Pacific-Asia Biodiversity Transect (PIBITRA; <http://www.botany.Hawaii.edu/pabitra>), Weed Risk Assessments for Hawaii and Pacific Islands (<http://www.botany.hawaii.edu/faculty/daehler/wra/>), the HAW herbarium, as well as an Electronic Theses and Dissertations library (<http://www.herbarium.hawaii.edu/collections/etd/>).

Sharing Databases

In the last few years, cooperation between a number of agencies has allowed databases to "talk to each other" through shared data fields. This includes the Hawai'i State Rare Plant database, the U.S. Army Pohakuloa and Oahu databases, the Hawai'i Biodiversity Mapping Program, and the NTBG databases. To protect the locations of extremely rare plants, these databases are not available to the public online.

Sharing On-ground Restoration Techniques

The HCC, discussed earlier, is the primary venue where restoration practitioners share their experience, expertise, and new technologies with all levels of the conservation community (<http://hawaiiconservation.org/activities/hawaii_conservation_conference>). Additionally, the HRPRG is a network of practitioners from conservation agencies and organizations, both public and private, that shares information on recovery efforts on all the islands and communicates through meetings, an online listserver, and a web site (<http://www.hear.org/hrprg/index.html>). This web site includes a bibliography for restoration genetics, with guidance on collection and restoration protocols. The group was instrumental in the creation of the PEP and the mid-elevation, rare plant nurseries on several islands. The HRPRG has functioned to develop appropriate procedures and policies for dealing with rare and endangered plants and their recoveries (<http://www.hear.org/hrprg/index.html>).

Close Cooperation and Partnerships between Agencies/Organizations

The mutual sharing of staff, equipment, training opportunities, helicopter time, etc., among organizations in Hawai'i is frequent and essential for accomplishing our goals. Collaboration-coalition types of efforts are almost the rule, rather than the exception, in Hawai'i. We mention just two excellent examples of this. The Hawai'i Association of Watershed Partnerships (HAWP; <http://hawp.org>) comprises watershed partnerships on each island. This organization includes both private and public landowners, conservation groups, and citizen groups, all of whom work collaboratively toward landscape-scale conservation. Also, The Nature Conservancy of Hawai'i (TNC) works to preserve native landscapes and intact habitats for all of Hawai'i's living resources through a system of preserves and collaborations with landowners (<http://www.nature.org/ourinitiatives/regions/northamerica/unitedstates/Hawaii/index.htm>). TNC of Hawai'i offers state-of-the-art management tools, achieving substantial results that include the fencing of thousands of acres of native forests. This provides the long-term protection of rare species against the damage caused by feral ungulates. They work extensively with landowners and partners from both the public and private sectors.

Conclusions

While Hawai'i has been recognized for over 200 years as possessing a unique flora, it is only over the past several decades that the level of endangerment has begun to be quantified. Numerous organizations and many dedicated and passionate individuals have been working for years to document and conserve Hawai'i's globally important biodiversity. Although these efforts have yielded results, the continuing trend toward increased endangerment raises concerns locally and nationally. We believe that the GSPC's 2010 Objectives and Targets are an ideal framework for Hawai'i to coordinate and monitor the work currently being done and to bring much needed international awareness to our situation. Based on what other nations have done to create a national strategy for plant conservation, we propose that the HCA should develop an HSPC modeled after the GSPC. This will provide an effective template for our conservation work and tie directly into the global efforts under the United Nations Convention on Biological Diversity. Since the United Nations declared this the Decade of Biodiversity, there is no better time for Hawai'i to do this than now.

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TAXONOMIC REVISION OF THE NEOTROPICAL SPECIES OF *ELAPHOGLOSSUM* SECT. *SQUAMIPEDIA* (DRYOPTERIDACEAE)[1]

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Abstract

Taxonomic keys, illustrations, descriptions, synonymy, distribution maps, and an index to collectors' names and numbers are given for the Neotropical taxa belonging to *Elaphoglossum* Schott ex J. Sm. sect. *Squamipedia* Mickel & Atehortúa. Eighteen taxa are recognized herein, consisting of 16 species, with one of the species, *E. peltatum* (Sw.) Urb., having three forms. Three new species are described: *E. anthracinum* A. Vasco, Mickel & R. C. Moran, *E. blepharis* A. Vasco, Mickel & R. C. Moran, and *E. rhomboideum* A. Vasco, Mickel & R. C. Moran. The following name is lectotypified: *Acrostichum flabellatum* Humb. & Bonpl. ex Willd. var. *sphenophyllum* Kunze. Four species are atypical in the genus by having divided laminae: *E. colombianum* (Maxon) Mickel and *E. moorei* (E. Britton) Christ have pinnately divided laminae, *E. peltatum* (Sw.) Urb. has isodichotomously divided laminae, and *E. tripartitum* (Hook. & Grev.) Mickel has ternately divided laminae. The Neotropical species of the section can usually be distinguished from other species of *Elaphoglossum* by long-creeping, green rhizomes; thin, translucent, light orange or brown rhizome scales; distichous leaves; paired peglike aerophores on each side of the rhizome slightly proximal to the petiole bases; a lack of phyllopodia; leaves that are typically < 15 cm long; and echinulate spores. One species, *E. nidiforme* Mickel, is atypical by its large size and short-creeping rhizomes but is included here in *Elaphoglossum* sect. *Squamipedia* based on previous molecular phylogenetic analyses. All Neotropical species of *Elaphoglossum* sect. *Squamipedia* are epiphytes, usually in middle- to high-elevation forests. The section is most diverse in the Andes from Colombia to Bolivia, where 17 taxa occur.

Resumen

Se presentan una clave, ilustraciones, descripciones, sinonimia, mapas de distribución y un índice de colectores por apellidos y números de colección para los taxones neotropicales pertenecientes a *Elaphoglossum* Schott ex J. Sm. sección *Squamipedia* Mickel & Atehortúa. De esta sección se reconocen 18 taxones que representan 16 especies. Dentro de una de las especies *E. peltatum* (Sw.) Urb., se reconocen tres formas. Se describen tres nuevas especies: *E. anthracinum* A. Vasco, Mickel & R. C. Moran, *E. blepharis* A. Vasco, Mickel & R. C. Moran y *E. rhomboideum* A. Vasco, Mickel & R. C. Moran. Se lectotipifica el nombre *Acrostichum flabellatum* Humb. & Bonpl. ex Willd. var. *sphenophyllum* Kunze. Cuatro de las especies dentro de la sección son atípicas en el género por tener láminas divididas: *E. colombianum* (Maxon) Mickel y *E. moorei* (E. Britton) Christ las tienen pinnadamente divididas, *E. peltatum* (Sw.) Urb. dicotómicamente divididas y *E. tripartitum* (Hook. & Grev.) Mickel ternadamente divididas. Las especies neotropicales de la sección usualmente pueden distinguirse de otras especies de *Elaphoglossum* por sus rizomas verdes largamente rastreros, escamas del rizoma delgadas y translucidas de color pajizo, marrón o naranja claro, hojas dísticas, aeróforos en forma de gancho a cada lado del rizoma casi proximales a la base del peciolo, filopodios ausentes, hojas típicamente menores a los 15 cm de largo y esporas equinuladas. Una especie, *E. nidiforme* Mickel, presenta una morfología atípica con hojas bastantes más largas y rizomas cortamente rastreros, sin embargo es incluida en el presente trabajo debido a que los análisis filogenéticos moleculares la ubican dentro de *Elaphoglossum* sección *Squamipedia*. Todas las especies neotropicales de *Elaphoglossum* sección *Squamipedia* son epífitas usualmente en bosques montanos o montano-altos. La sección es más diversa en los Andes, desde Colombia hasta Bolivia, en donde puenden encontrarse 17 taxones.

Key words: Dryopteridaceae, *Elaphoglossum*, IUCN Red List, Neotropics.

Elaphoglossum Schott ex J. Sm. is one of the world's largest fern genera, containing ca. 600 species, probably ca. 100 of which remain undescribed. It is a member of the Dryopteridaceae (Smith et al., 2006), and within that family belongs to the bolbitidoid clade characterized by creeping rhizomes,

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elongate (as seen in cross section) ventral meristeles, a lack of hairs, sterile-fertile leaf dimorphy, and acrostichoid sori (Moran et al., 2010a, 2010b). Its sister genus is *Mickelia* R. C. Moran, Labiak & Sundue (Moran et al., 2010a, 2010b). Unlike other species-rich fern genera, *Elaphoglossum* is relatively uniform morphologically. Nearly all of its species have simple, entire laminae and free veins. Most of the characters used to distinguish the species are based on the scales of the rhizomes and leaves, the shape of the laminae, and the presence or absence of hydathodes and phyllopodia (Mickel & Atehortúa, 1980). We estimate that ca. 80% of the species are epiphytes.

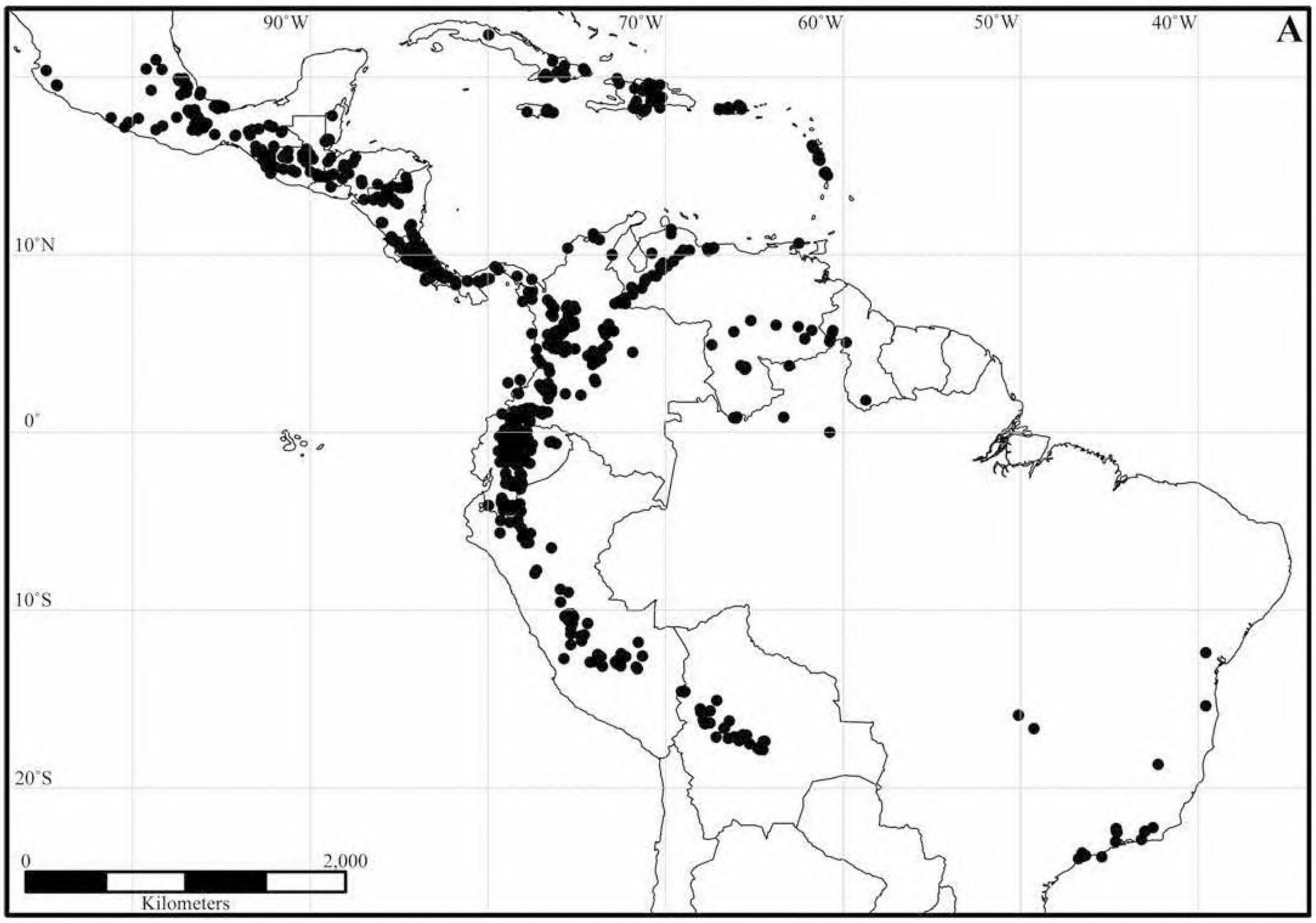
The present paper is one in a series of monographs for clades within *Elaphoglossum* (Vasco et al., 2009a, 2009b; Vasco, 2011) and floristic treatments for large geographical areas (Mickel & Beitel, 1988; Mickel, 1991, 1995a, 1995b; Mickel & Smith, 2004). We present a taxonomic revision of the 18 Neotropical taxa that we assign to *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa (Appendix 1). This section was first recognized by Mickel and Atehortúa (1980). Subsequently, the monophyly of the section has been supported by noncoding chloroplast DNA sequences (Rouhan et al., 2004; Skog et al., 2004). The morphological synapomorphies supporting the monophyly of the section are the absence of phyllopodia (Mickel & Atehortúa, 1980) and echinulate spores (Moran et al., 2007). Other morphological characteristics that are uniform or nearly so within the section, but are apparently plesiomorphic, are long-creeping rhizomes, paired peglike aerophores (Figs. 3B, 8B), and 2-ranked leaves (Mickel & Atehortúa, 1980).

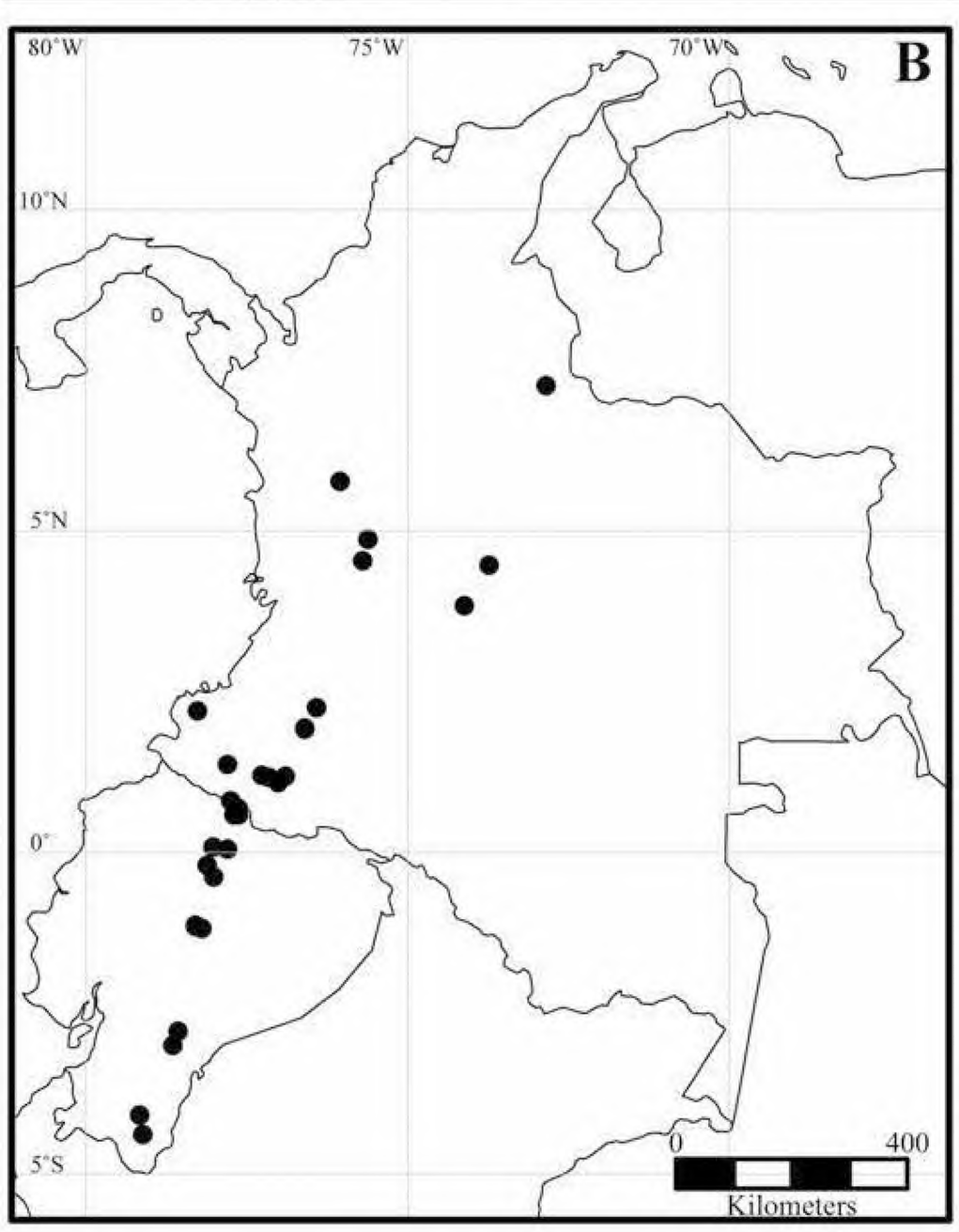
Another possible synapomorphy for *Elaphoglossum* sect. *Squamipedia* might be the chromosome number. Wagner (1980) found that one species of the section, *E. peltatum* (Sw.) Urb. f. *peltatum*, had $x = 40$, not $x = 41$ as in the rest of the genus and for dryopteroid ferns in general (Smith et al., 2006). Wagner's count is the only one available for the section. It has been confirmed by a count of another individual of *E. peltatum* f. *peltatum* collected at La Selva Biological Station in Costa Rica (Fernando Matos, pers. comm.). Whether $x = 40$ is constant within *Elaphoglossum* sect. *Squamipedia* needs further investigation.

Gametophytes might also exhibit another synapomorphy for the section. Stokey and Atkinson (1957) examined the gametophytes of two species of *Elaphoglossum* sect. *Squamipedia* (*E. peltatum* f. *peltatum* and *E. tripartitum* (Hook. & Grev.) Mickel [*Bell 662*, COL]) and 18 species from *Elaphoglossum* sections *Elaphoglossum*, *Lepidoglossa* Christ, and *Setosa* (Christ) Mickel & Atehortúa. All the gametophytes developed slowly and when mature were long, narrow, ribbon shaped, and beset with marginal rhizoids. This morphology was later corroborated by Chiou et al. (1998) for other members of the genus. All of the species examined by Stokey and Atkinson (1957) bore 1-celled papillate hairs with waxy caps except for the two species of *Elaphoglossum* sect. *Squamipedia* examined, which lacked such hairs entirely. We can confirm this with a form of *Elaphoglossum* sect. *Squamipedia* (*E. peltatum* f. *peltatum*) that we grew from spores. Thus, the absence of papillate hairs may be a synapomorphy for *Elaphoglossum* sect. *Squamipedia*, but more species in the section should be examined to verify this.

Within *Elaphoglossum*, a genus composed almost entirely of species with simple and entire laminae, *Elaphoglossum* sect. *Squamipedia* is of special interest because four of its species have dissected laminae (see next paragraph). Elsewhere in the genus, dissected laminae occur in only two species belonging to two sections: *E. bifurcatum* (Jacq.) Mickel, belonging to *Elaphoglossum* sect. *Lepidoglossa* (Vasco et al., 2009a, 2009b), and *E. cardenasii* W. H. Wagner, which belongs to *Elaphoglossum* sect. *Setosa* (Wagner, 1954; Mickel & Atehortúa, 1980; Rouhan et al., 2004, 2007). The species of *Elaphoglossum* with dissected laminae have sometimes been classified in segregate genera, namely *Microstaphyla* C. Presl, *Peltapteris* Link, and *Rhipidopteris* Schott ex Fée nom superfl. (Morton, 1955; Gómez, 1975; Mickel, 1995a). Because these segregates are nested within *Elaphoglossum* (Rouhan et al., 2004, 2007; Vasco et al., 2009b), they are no longer recognized because doing so would leave *Elaphoglossum* paraphyletic.

Within *Elaphoglossum* sect. *Squamipedia* there are three different patterns of laminar division. First, a dichotomous pattern is found in *E. peltatum* f. *peltatum* and *E. peltatum* f. *standleyi* (Maxon) Mickel, where the lamina bifurcates at the apex of the petiole to form two equal lamina halves. Any subsequent divisions of the two lamina halves—there may be up to seven divisions—are also dichotomous. Second, a pinnate plan, found in *E. colombianum* (Maxon) Mickel and *E. moorei* (E. Britton) Christ, has the rachis as a straight extension of the petiole (i.e., the petiole is not bifurcated at the apex) and five to 17 pairs of lateral pinnae borne along the rachis. Finally, there is a ternate plan, as in *E. tripartitum*, where the petiole and rachis form one continuous axis (i.e., the petiole is not bifurcated at the apex) and the lamina divides into three equal parts: two lateral pinnae and a central terminal portion. Our unpublished molecular phylogenetic results using three chloroplast markers (Vasco et al., in prep.) have found that the





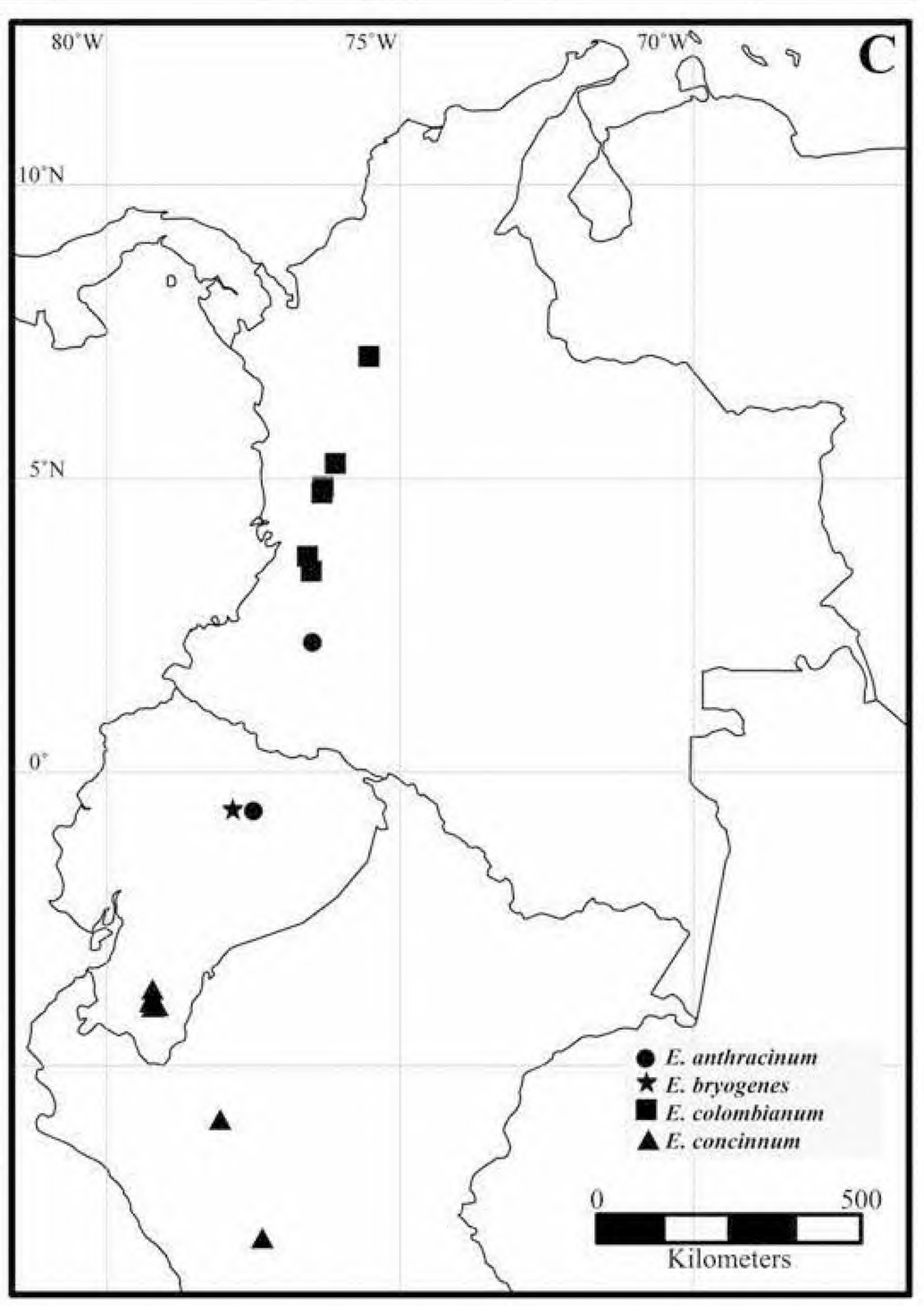


Figure 1. Distribution maps. —A. An overview of *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa in the New World. —B. *Elaphoglossum andreanum* Christ. —C. *Elaphoglossum anthracinum* A. Vasco, Mickel & R. C. Moran (●), *Elaphoglossum bryogenes* Mickel (★), *Elaphoglossum colombianum* (Maxon) Mickel (■), and *E. concinnum* Mickel (▲).

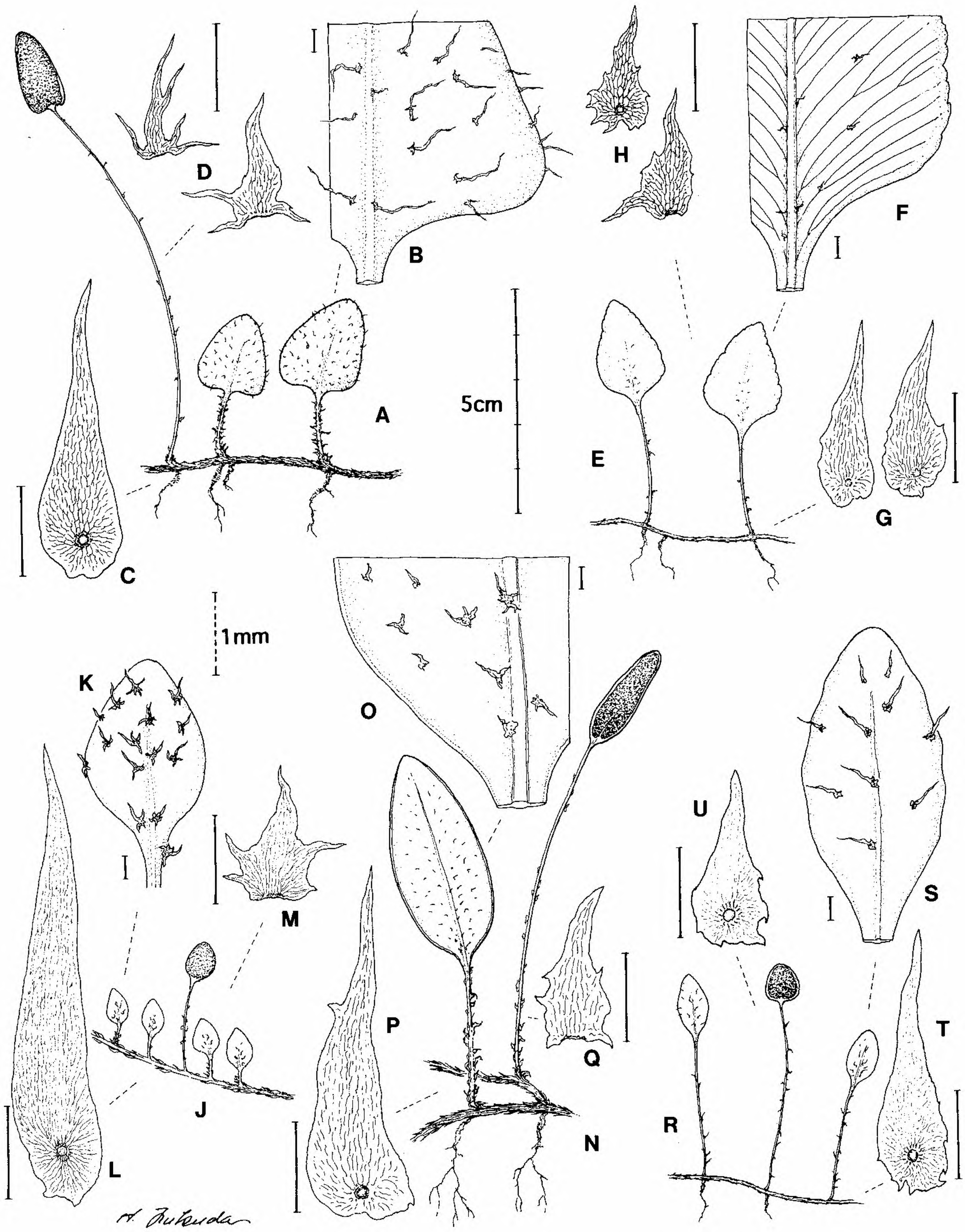


Figure 2. A–D. *Elaphoglossum blepharis* A. Vasco, Mickel & R. C. Moran. —A. Habit, with fertile leaf at left, two sterile at right. —B. Adaxial lamina detail. —C. Rhizome scale. —D. Petiolar scales. E–H. Juvenile leaves of *E. lloense* (Hook.) T. Moore. —E. Habit. —F. Abaxial lamina detail. —G. Rhizome scales. —H. Petiolar scales. J–M. *Elaphoglossum bryogenes* Mickel. —J. Habit, with five leaves, the dimorphic fertile one at center. —K. Adaxial lamina detail. —L. Rhizome scale. —M. Petiolar scale. N–Q. *Elaphoglossum squamipes* (Hook.) T. Moore. —N. Habit, sterile leaf to left, fertile to right. —O. Adaxial lamina detail. —P. Rhizome scale. —Q. Petiolar scale. R–U. *Elaphoglossum concinnum* Mickel. —R. Habit, fertile leaf at center. —S. Adaxial lamina detail. —T. Rhizome scale. —U. Petiolar scale. A–D from *Harling & Andersson 18092* (AAU); E–H from *Hoover et al. 2897* (MO); J–M from *Luteyn & Sylva 14682* (NY); N–Q from *Brade 5290* (NY); R–U from the holotype *Young 1301* (NY). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.

four species of *Elaphoglossum* sect. *Squamipedia* with divided laminae are not monophyletic; instead they have had independent origins from ancestors with simple, entire laminae.

The original circumscription of *Elaphoglossum* sect. *Squamipedia* by Mickel and Atehortúa (1980) has been modified as a result of molecular phylogenetic studies. Rouhan et al. (2004) found that *E. ovatum* (Hook. & Grev.) T. Moore, originally assigned to the section by Mickel and Atehortúa (1980), belongs to *Elaphoglossum* sect. *Lepidoglossa*. Rouhan et al. (2007) also found that two species endemic to Madagascar, *E. marojejyense* Tardieu and *E. nidusoides* Rouhan & Rakotondr., are sister to the Neotropical species of *Elaphoglossum* sect. *Squamipedia*. The two Madagascan species were considered by Rouhan et al. (2004, 2007) to belong to *Elaphoglossum* sect. *Squamipedia*. Both species, however, differ morphologically in certain respects from the Neotropical species. *Elaphoglossum marojejyense* resembles the Neotropical species in its creeping rhizomes, distichous leaves, small size, and the presence of paired aerophores; however, it differs by perispores lacking many small spines, as found in Neotropical members of the section (Moran et al., 2007). Similarly, the second species, *E. nidusoides*, is aberrant morphologically in *Elaphoglossum* sect. *Squamipedia*. It appears to be a typical member of *Elaphoglossum* sect. *Elaphoglossum* by its compact rhizomes, presence of phyllopodia, larger leaves, near or total lack of laminar scales, and cristate perispores (Rouhan et al., 2007). Besides these two Madagascan endemics, Rouhan et al. (2007) also found that an Andean species, *E. nidiforme* Mickel, was nested in the section. The species resembles *E. nidusoides* from Madagascar and, similarly, is atypical morphologically in *Elaphoglossum* sect. *Squamipedia*. It more closely resembles species of *Elaphoglossum* sect. *Elaphoglossum* in its large leaves, short-creeping rhizomes, and presence of phyllopodia (it is the only Neotropical member of *Elaphoglossum* sect. *Squamipedia* that has phyllopodia). However, we have found that its spores are like those of Neotropical members of *Elaphoglossum* sect. *Squamipedia*, having echinulate perispores. In our present treatment of *Elaphoglossum* sect. *Squamipedia*, *E. nidiforme* is included on the basis of molecular evidence (Vasco et al., in prep.), even though it seems atypical morphologically.

Besides the study by Rouhan et al. (2007), our own molecular phylogenetic study (Vasco et al., in prep.) has found that *Elaphoglossum wrightii* (Mett. ex D. C. Eaton) T. Moore, a species originally placed in the section by Mickel and Atehortúa (1980), does not belong to *Elaphoglossum* sect. *Squamipedia* and is accordingly excluded from the section (see Excluded Species).

Materials and Methods

This study is based on an examination of over 3000 herbarium sheets representing ca. 1300 individual collections from 27 herbaria (see footnote first page). For most of the specimens, geographic coordinates were estimated using geographical gazetteers because this information was often not provided on the labels. These estimated coordinates were used to compose the distribution maps for the species and are given in brackets for type and paratype specimens cited below. Illustrations and silhouette images were prepared from herbarium specimens.

Available at the *Elaphoglossum* pages at <http://sweetgum.nybg.org/elaphoglossum/index.php> are the descriptions and discussions for the species included in this monograph. Also available at the web site is information on all specimens examined (also available from the author upon request), photographs of all types and of selected specimens, copies of all protologues, and additional photographs. A list of all names, both accepted and synonyms, are listed in Appendix 2. A list of all specimens examined, with collectors' names and numbers, is given in Appendix 3.

Taxonomic Treatment

I. Elaphoglossum sect. **Squamipedia** Mickel & Atehortúa, Amer. Fern J. 70: 57. 1980. TYPE: *Acrostichum squamipes* Hook. [≡ *Elaphoglossum squamipes* (Hook.) T. Moore]. Figure 1A.

Peltapteris Link, Fil. Spec. 147. 1841. *Elaphoglossum* subsect. *Peltapteris* (Link) Mickel & Atehortúa [in *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa], Amer. Fern J. 70: 59. 1980. TYPE: *Osmunda peltata* Sw. [≡ *Elaphoglossum peltatum* (Sw.) Urb. f. *peltatum*].

Rhipidopteris Schott ex Fée, Mem. Foug. [Hist. Acrost.] 2: 14. 1845, nom. superfl. for *Peltapteris* and with the same type [see Morton, 1955]. TYPE: *Acrostichum peltatum* (Sw.) Sw. [≡ *Elaphoglossum peltatum* (Sw.) Urb.]

Elaphoglossum subsect. *Feeana* Christ [in *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa], Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 60. 1899. TYPE: *Acrostichum feei* Bory ex Fée [≡ *Elaphoglossum feei* (Bory ex Fée) T. Moore].

Rhizomes typically 1–1.5 mm wide (to 10 mm wide in *Elaphoglossum nidiforme*), slender, long-creeping or (in *E. nidiforme*) short-creeping to compact;

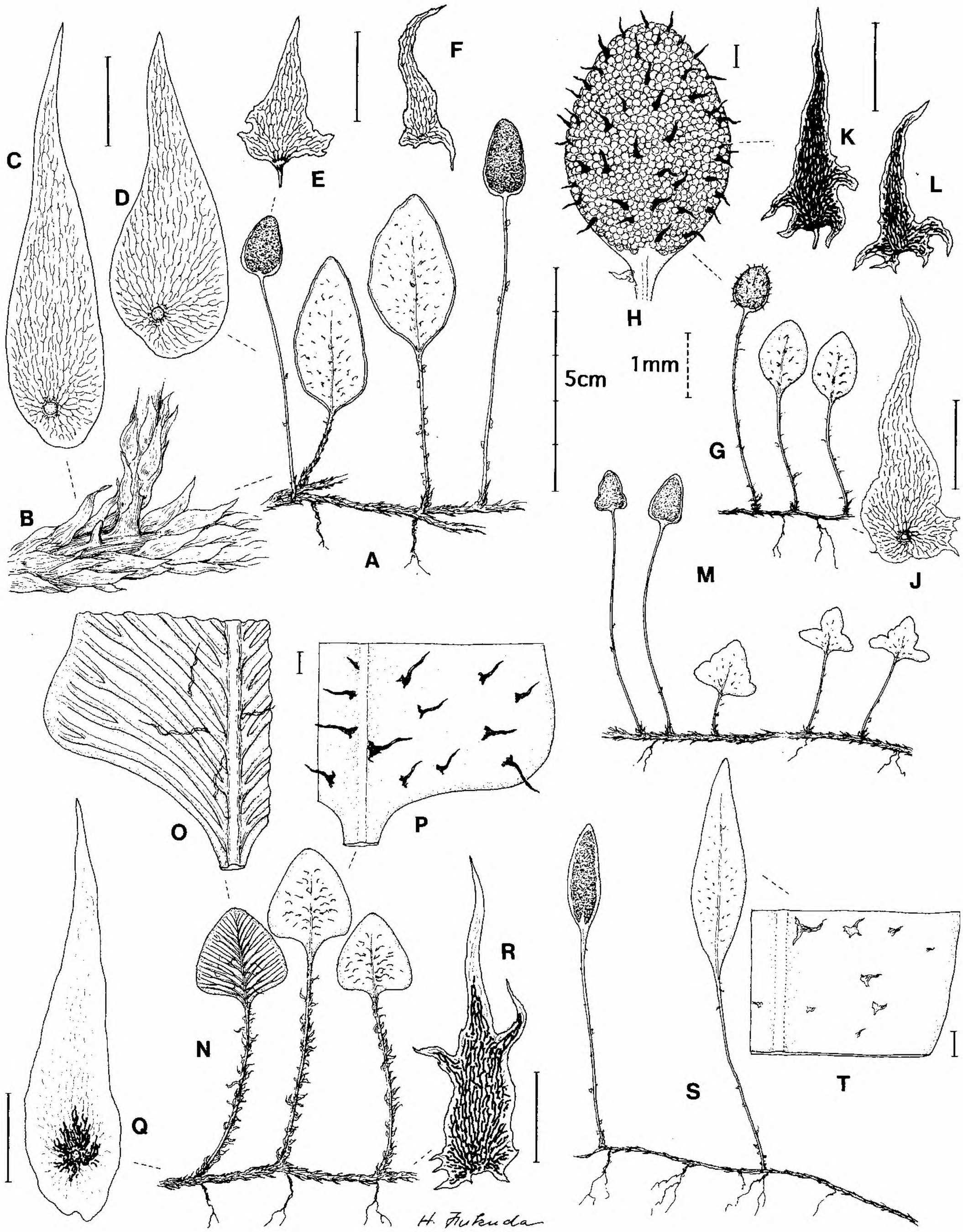


Figure 3. A–F. *Elaphoglossum squamipes* (Hook.) T. Moore. —A. Habit, with two sterile leaves at center, fertile left and right. —B. Rhizome detail with aerophore. —C. Rhizome scale. —D. Petiolar scale. —E. Intersporangial scale. —F. Laminar scale. G–L. *Elaphoglossum concinnum* Mickel. —G. Habit, fertile leaf at left. —H. Fertile lamina detail. —J. Rhizome scale. —K, L. Fertile laminar scales. —M. *Elaphoglossum deltoideum* (Sodiro) Christ. Habit, with two fertile leaves at left, three sterile at right. N–R. *Elaphoglossum anthracinum* A. Vasco, Mickel & R. C. Moran. —N. Habit, all leaves are sterile. —O. Abaxial lamina detail. —P. Adaxial lamina detail. —Q. Rhizome scale. —R. Petiolar scale. S, T. *Elaphoglossum lloense* (Hook.) T. Moore. —S. Habit, with fertile leaf at left. —T. Abaxial lamina detail. A–F from *Breedlove 22733* (NY); G–L from *van der Werff & Palacios 9054* (MO); M from *Holm-Nielsen & Jeppesen 1365* (AAU); N–R from the holotype, *Luteyn & Cotton 11002* (NY); S, T from *Øllgaard & Navarrete 2700* (AAU). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.

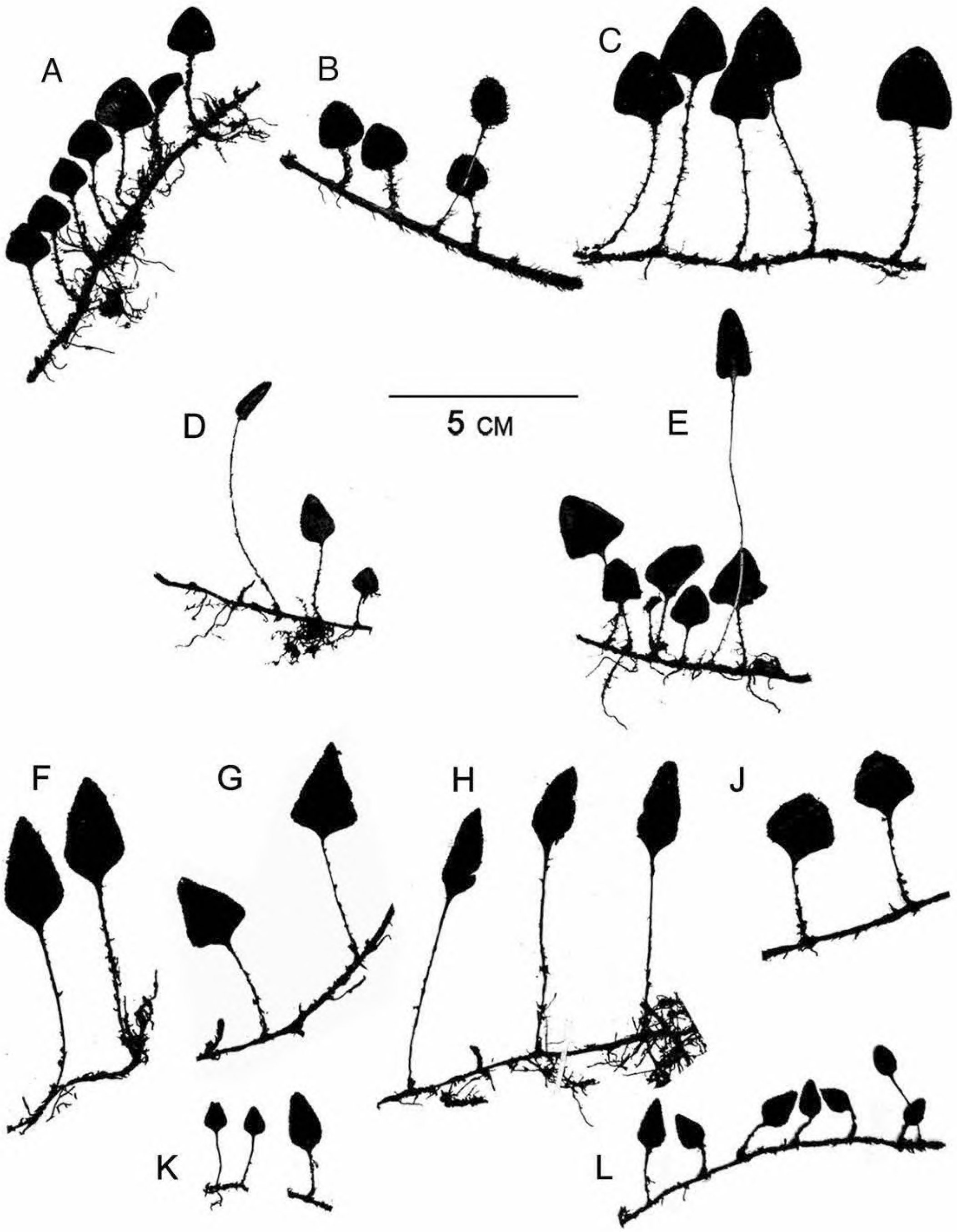


Figure 4. Silhouettes of three species of *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa. A–C. *Elaphoglossum anthracinum* A. Vasco, Mickel & R. C. Moran. D, E. *Elaphoglossum blepharis* A. Vasco, Mickel & R. C. Moran. F–L. *Elaphoglossum andreanum* Christ. A from *Luteyn & Cotton 11002* (MO); B from *Lozano 3489* (COL); C from *Luteyn & Cotton 11002* (NY); D from *Harling & Andersson 22455* (AAU); E from *Harling & Andersson 18092* (AAU); F from *Velez et al. 4206* (COL); G from *van der Werff & Palacios 10621* (MO); H from *Jaramillo et al. 5973* (COL); J from *Lozano et al. 4684* (COL); K from *Moran 6867* (NY); L from *André 3114* (NY).

rhizome scales narrowly lanceolate to ovate, light orange to brown, sometimes darkened at point of attachment; aerophores paired, peglike, ca. 1 mm tall, whitish to yellowish or greenish, borne on the rhizome about 1–2 mm proximal to the petiole base, one on each side of the petiole base (absent in *E. nidiforme*). Sterile leaves generally < 15 cm long (to 30–37 cm long in *E. nidiforme*), distichous, alternate, distant; petiolar scales ovate to lanceolate, peltate, hastate; phyllopodia generally absent; laminar scales often hastate with 1 to several basal processes or projections; veins free, simple or once-forked; hydathodes lacking. Perispores echinulate, with broad continuous folds or ridges. Chromosome number: $x = 40$ (Wagner, 1980).

Distribution. *Elaphoglossum* sect. *Squamipedia* is most diverse in the Andes from Colombia to Bolivia, where 17 taxa occur. Three taxa occur in Mexico, five in Central America, three in the Antilles, and two in the coastal mountains of southeastern Brazil (Appendix 4).

Key to the Neotropical Species of *Elaphoglossum* sect. *Squamipedia*

Note: Leaf measurements were taken from the largest leaf on each herbarium sheet. Examples of our definitions of lamina shape: deltate (Fig. 4C), deltate-hastate (Fig. 5L), elongate deltate (Fig. 4F), elliptic (Fig. 10E), rhomboid (Fig. 5G).

1. Rhizomes compact; sterile leaves 30–37 × 4–5 cm; phyllopodia present ..... *E. nidiforme*
1′. Rhizomes long-creeping; sterile leaves 1–15(–27.5) × 0.5–3(–4) cm; phyllopodia absent 2
2. Sterile laminae divided 3
3. Sterile laminae dichotomously divided (divided at the apex of the petiole into 2 equal parts) 4
4. Sterile laminae divided 1 or 2 times ..... *E. peltatum* f. *flabellatum*
4′. Sterile laminae divided 3 to 7 times ..... *E. peltatum* f. *peltatum*
3′. Sterile laminae pinnately divided 5
5. Sterile laminae ternate or biternate; northwestern Ecuador ..... *E. tripartitum*
5′. Sterile laminae pinnate with 5 to 17 pairs of pinnae; Colombia, Peru, Bolivia 6
6. Pinna pairs 5 to 9; pinna bases 1–2 mm wide; western Colombia ..... *E. colombianum*
6′. Pinna pairs 8 to 17; pinna bases 0.4–1 mm wide; Peru, Bolivia ..... *E. moorei*
2′. Sterile laminae simple 7
7. Sterile laminae 0.3–0.8 cm wide, very narrowly elliptic, crenate; Lesser Antilles (Dominica, Guadeloupe) ..... *E. feei*
7′. Sterile laminae 0.4–4 cm wide, broadly deltate or ovate to rhombic, lanceolate, oblanceolate or elliptic, entire or minutely crenulate; Greater Antilles (Cuba, Jamaica, Dominican Republic), Mexico, Central America, South America 8
8. Sterile laminae (3)5–27.5 cm long, (1.8 to)3 to 14 times longer than wide, ovate-lanceolate, elliptic or oblong 9
9. Sterile lamina apices attenuate, acute to acuminate ..... *E. lloense*
9′. Sterile lamina apices obtuse to broadly acute 10
10. Sterile laminae (3 to)4 to 11 times longer than wide, narrowly elliptic to oblong, usually widest at or above the middle, often parallel-sided medially; at elevations from 100 to 1000(1700) m ..... *E. minutum*
10′. Sterile laminae 1.8 to 2.5(to 4) times longer than wide, ovate-lanceolate or spatulate, usually widest below the middle; at elevations from (800)1700 to 3800 m ..... *E. squamipes*
8′. Sterile laminae 0.8–3.5 cm long, 0.8 to 2.5 times longer than wide, lunate, deltate, ovate, elongate deltate, elliptic, or rhombic 11
11. Sterile laminae lunate or flabellate ..... *E. peltatum* f. *standleyi*
11′. Sterile laminae deltate or elongate deltate, ovate, rhombic, elliptic, or lanceolate 12
12. Sterile laminae rhombic 13
13. Sterile laminae 0.4–0.7 cm wide; at elevations from 1800 to 2100 m ..... *E. bryogenes*
13′. Sterile laminae 0.9–1.9 cm wide; at elevations from 2400 to 3200 m ..... *E. rhomboideum*
12′. Sterile laminae elliptic, deltate, or elongate deltate 14
14. Scales on the abaxial surface of the sterile laminae black throughout, or black only at point of attachment, or at the apex 15
15. Sterile laminae minutely crenulate, typically elongate-deltate ..... *E. andreanum*
15′. Sterile laminae entire, elliptic to deltate 16
16. Scales on the abaxial surface of the sterile laminae 1–2 mm long; sterile laminae elliptic, short-decurrent ..... *E. concinnum*
16′. Scales on the abaxial surface of the sterile laminae 2.5–3 mm long; sterile laminae deltate, truncate ..... *E. anthracinum*
14′. Scales on the abaxial surface of the sterile laminae orange or light to dark brown 17
17. Sterile laminae entire 18

18. Scales on the adaxial surface of the sterile laminae linear, the bases hastate by linear processes, scales on the abaxial surface of the sterile laminae 0.3–1.2 mm ..... *E. blepharis*
18′. Scales on the adaxial surface of the sterile laminae narrowly lanceolate, scales on the abaxial surface of the sterile laminae 1–2 mm ..... *E. concinnum*

17′. Sterile laminae minutely crenulate 19
19. Sterile laminae deltate or deltate-hastate ..... *E. deltoideum*
19′. Sterile laminae elongate-deltate ..... *E. andreanum*

1. Elaphoglossum andreanum Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36: 100, fig. 80. 1899. TYPE: Colombia. Nariño: cordillera Oriental, Alto del Tábano in Andibus Pastoensibus, [1°48″S, 78°35″W], 3200 m, 4 Mar. 1876, *E. André 3114* (holotype, P not seen, P photos GH!, NY!; isotypes, B!, GH!, NY!). Figures 1B, 4F–L.

Rhizomes 1 mm wide, long-creeping; rhizome scales 3–5 mm, appressed, lanceolate, entire, light orange to brown, concolorous or with dark point of attachment, dull. Sterile leaves 2.6–9.5 cm; petioles 0.9 to 2.2 times the lamina length; petiolar scales 1.5–3 mm, scattered, lanceolate, light orange to brown, concolorous or black at point of attachment; laminae 1–3.5 × 0.6–2 cm, 1.1 to 2.1 times longer than wide, coriaceous, simple, slightly elongate, deltate or rarely narrowly rhombic, margins minutely crenulate, rarely (in small specimens) entire, apices rounded, bases truncate; adaxial lamina surface scaly, the scales 0.5–1.5 mm, ovate to lanceolate, often hastate at base and sometimes with lateral processes as long as the length of the scale, usually light orange to dark brown or black; abaxial lamina surface scaly, the scales (0.2–) 0.7–1.5 mm, ovate to lanceolate, often hastate at the base, sometimes with lateral processes as long as the length of the scale, sometimes the scales reduced to ca. 0.2 mm and circular or stellate, light orange (sometimes black at point of attachment) to dark brown or black. Fertile leaves 2.7–7.5 cm; petioles 2 to 3 times the lamina length; laminae 0.9–2.3 × 0.7–1.9 cm, ovate to slightly oblong, entire, apices broadly acute to rounded, bases slightly cordate to truncate or broadly cuneate; intersporangial scales 0.5–2 mm, light brown to dark brown or black.

Distribution and elevation. *Elaphoglossum andreanum* occurs in Colombia and Ecuador; specimens have been collected at elevations from 2800 to 3700 m.

Discussion. *Elaphoglossum andreanum* is characterized by small leaves not exceeding 9.5 cm and slightly elongate-deltate laminae with minutely crenulate margins. It occurs at higher elevations than most other species of *Elaphoglossum* sect. *Squamipedia*, which are generally found between 1500 and 3000 m. The species resembles *E. concinnum* Mickel, which differs by more elliptic or rhombic laminae, broadly obtuse lamina apices, and occurrence at slightly lower elevations (2450–3000 m, southern Ecuador and Peru). Also similar is *E. squamipes*, which differs by laminae 1.8 to 2.5(to 4) times longer than wide, lanceolate or elliptic and entire (rarely minutely crenulate, and only in small laminae). See *E. anthracinum* A. Vasco, Mickel & R. C. Moran, *E. blepharis* A. Vasco, Mickel & R. C. Moran, *E. bryogenes* Mickel, *E. rhomboideum* A. Vasco, Mickel & R. C. Moran, and *E. squamipes* for morphological comparisons to those species.

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Bolivar, *Rodríguez et al. 4692* (HUA, NY). **Cauca:** macizo Colombiano, páramo de las Papas, alrededor de la laguna de Cusiyaco, *Barclay 5969* (COL, GH, MO); Par. Nac. Nat. Puracé, sitio Peña Amarilla, al S de la laguna San Rafael, *Duque 162* (COL). **Cundinamarca:** Mpio. de Fomeque, páramo de Chingaza, *Huertas & Camargo 5928* (COL). **Huila:** Depto. Huila-Cauca, macizo Colombiano, páramo de Las Papas, cerros y alrededores de la laguna La Magdalena, *Idrobo et al. 2992* (COL, NY). **Meta:** cerro Nevado del Sumapaz, quebrada El Buque, *Cleef 7839* (COL). **Nariño:** páramo del Tábano, alto de la cordillera entre Pasto y El Encanto, vertiente W, *Cuatrecasas 11911* (COL, F); páramo El Tábano al E de Pasto, *Hagemann & Leist 1359* (COL); Mpio. de Pasto, Correg. El Encano, El Motilón–El Socorro, *Ramírez 2822* (COL). **Putumayo:** Mpio. de Santiago, vereda de San Antonio de Bellavista, páramo de Bordoncillo, *Ramírez et al. 4721* (COL); valle de Sibundoy, *Schultes & Cabrera 20100* (COL, NY). **Quindío:** Mpio. de Salento, Est. Biol. Estrella de Agua, camino hacia el Alto del Colmillo, *Vélez et al. 4206* (COL). **Risaralda:** Mpio. de Sta. Rosa, entre la Hacienda La Sierra y Termales de Sta. Rosa, quebrada La Sierra, *Jaramillo-M. et al. 5919* (COL), *5973* (COL). **Santander:** W slope of páramo Rico, *Killip & Smith 17867* (GH, NY). **Unknown:** *Lehmann 4928* (K).

ECUADOR. **Carchi:** Above La Esperanza, 5 km W of El Carmelo on rd. to Tulcán, *Løjtnant et al. 12069* (AAU); Est. Biol. La Guandera, *Moran et al. 6867* (NY, QCA, QCNE); ca. 1/2 hr. E of Huaca, past Colonia Huaceña, *van der Werff & Palacios 10621* (AAU, MO, NY, UC). **Imbabura:** boggy areas E of Cayambe Peak, *Wiggins 10423* (NY). **Loja:** Cerro Toledo, E of Yangana, betw. Loja & Valladolid, *Lehnert 1460* (NY, UC); Par. Nac. Podocarpus E of Nudo de Cajanuma, trail from "centro de informacion" toward Lagunas de Compadre, *Øllgaard 90336* (AAU, QCA, QCNE). **Morona-Santiago:** rd. Gualaceo–Plan de Milagro, 3.8 km E of pass, *Øllgaard & Navarrete 2797* (AAU); Muletrack Sevilla de Oro–Mendez, E slope at Cerro Negro, El Castillo, *Øllgaard &*

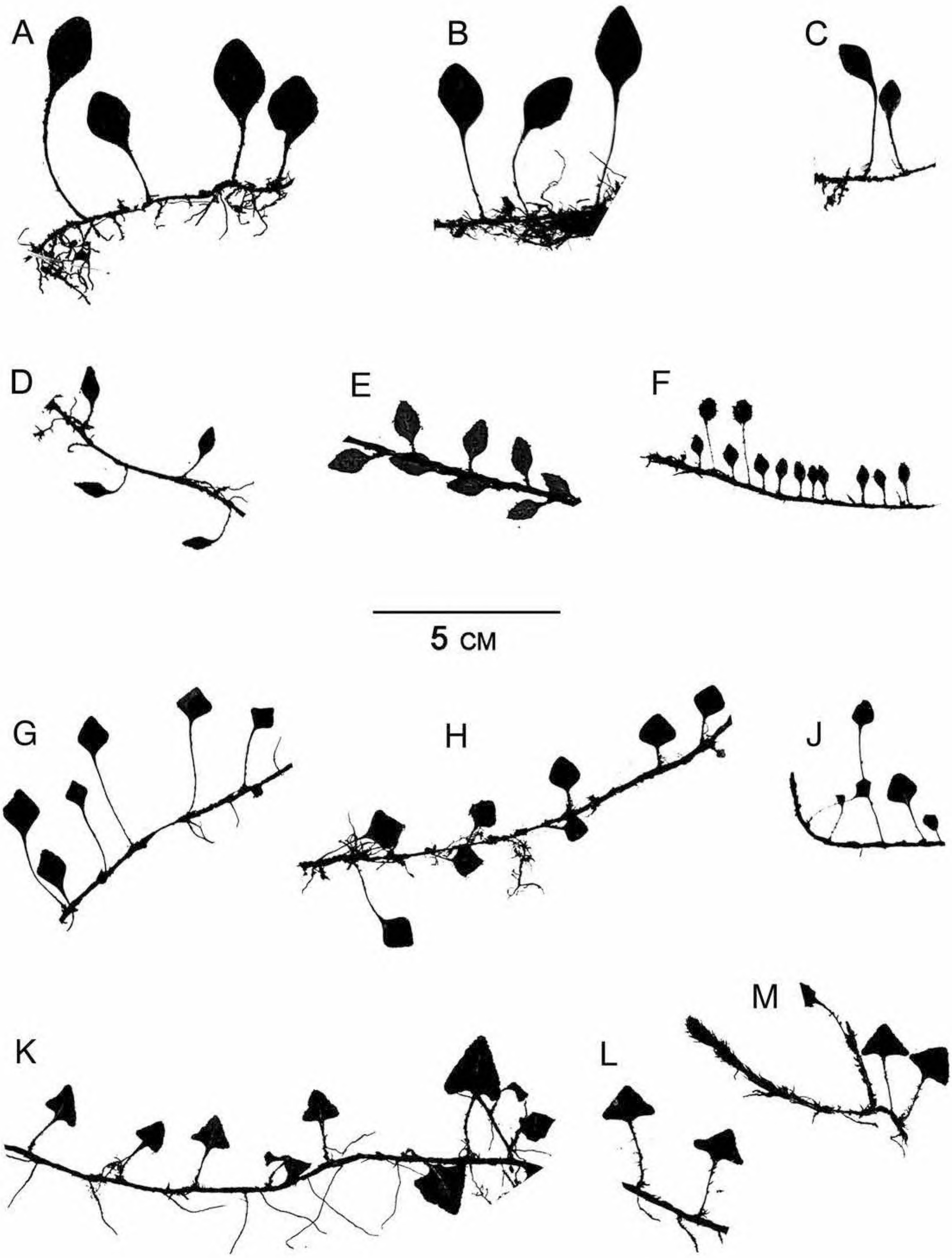
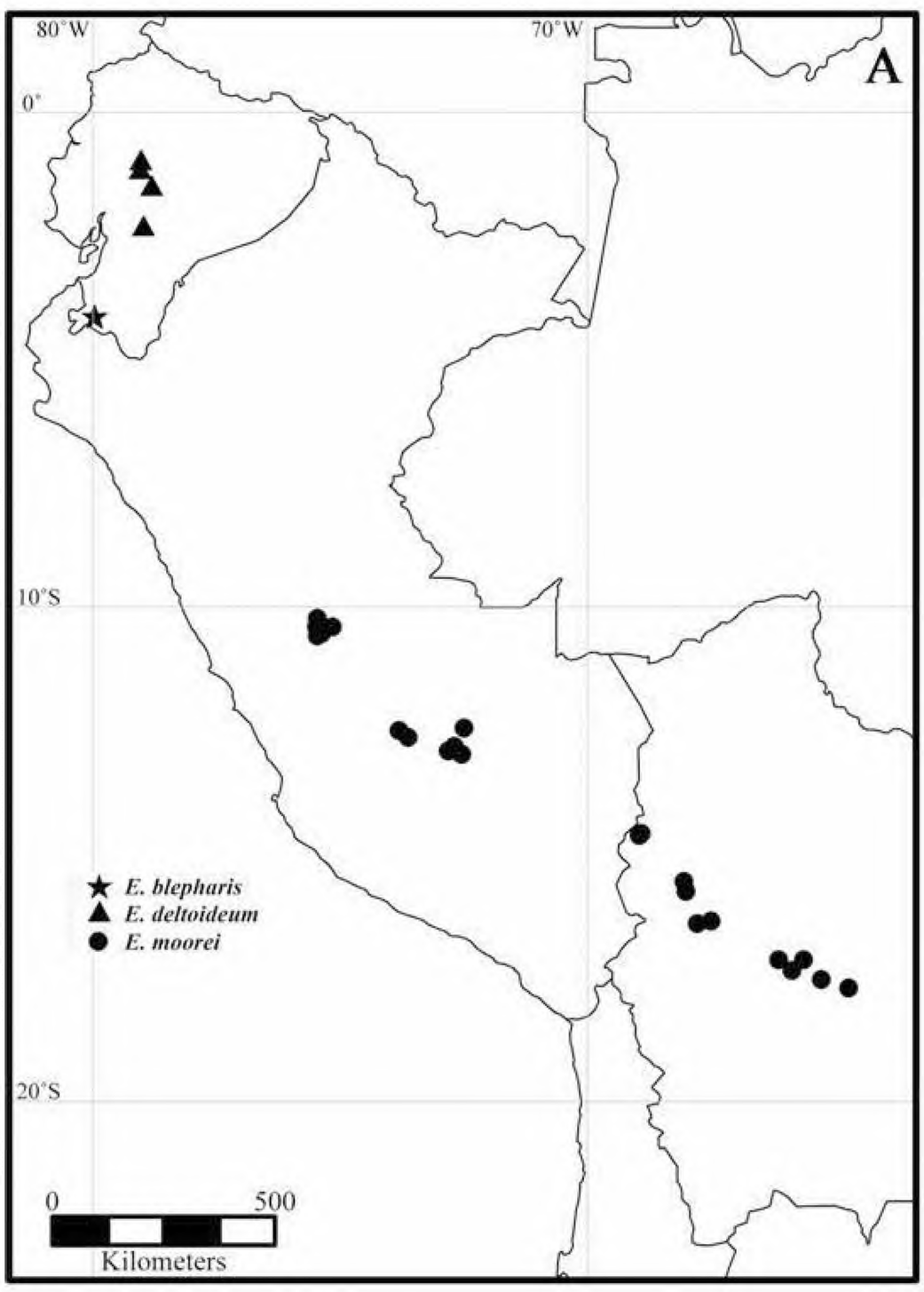
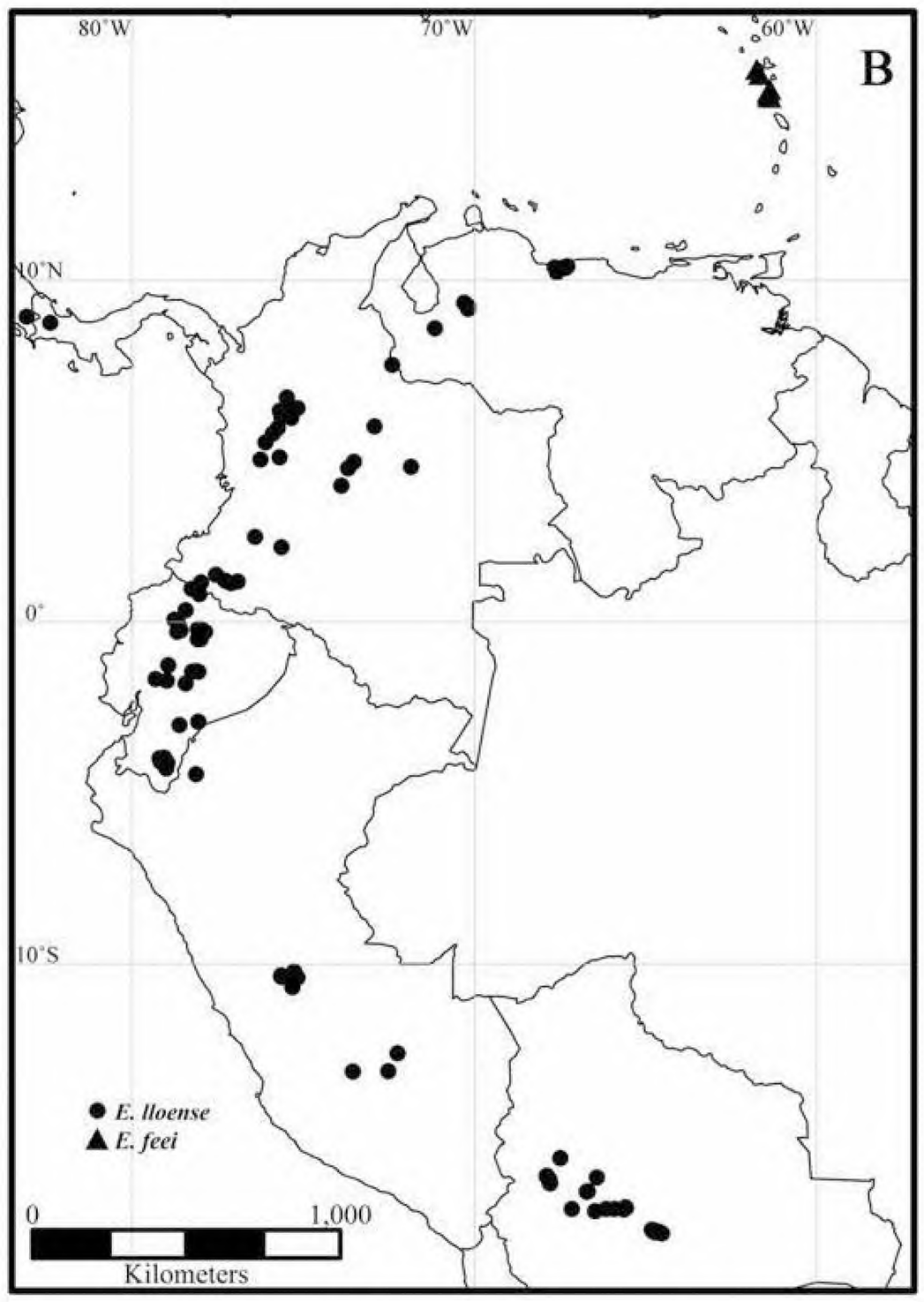
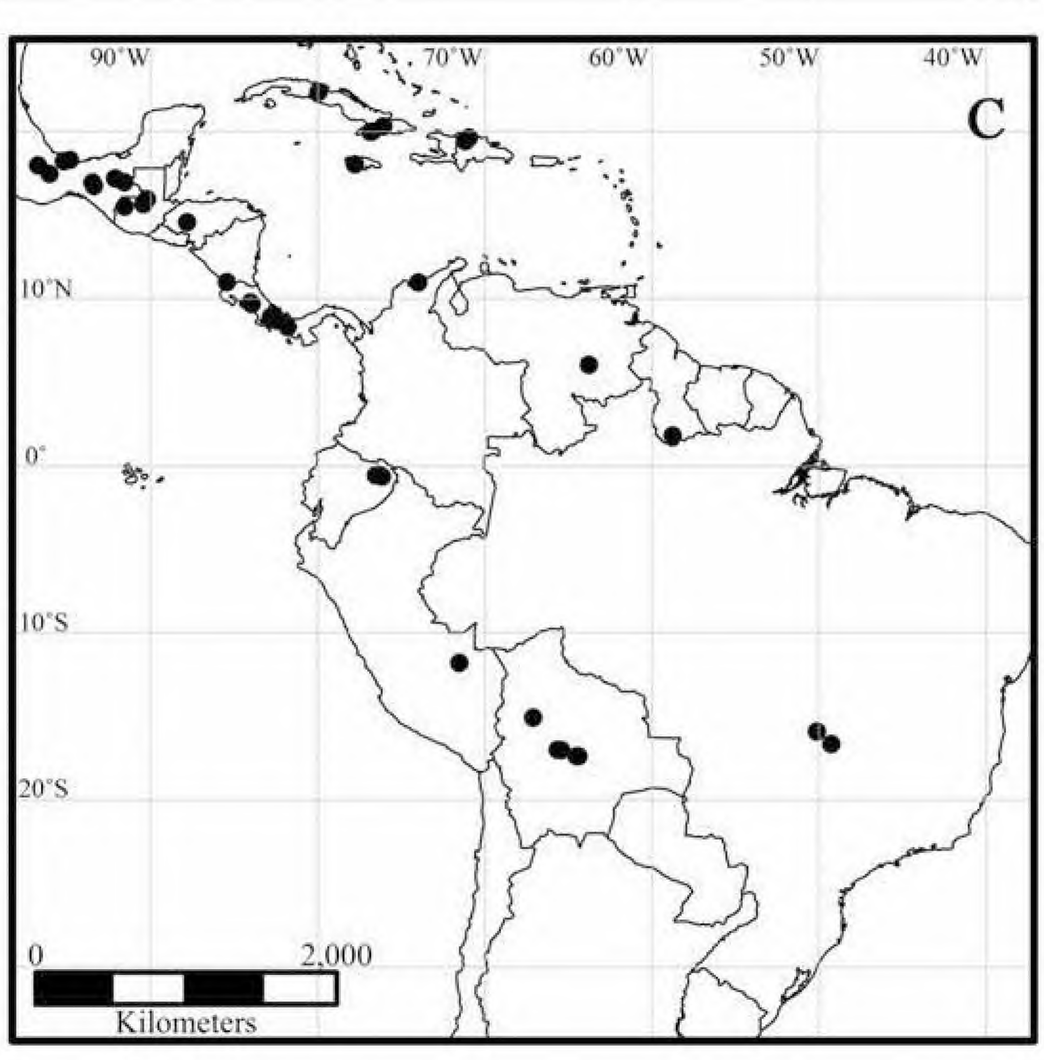


Figure 5. Silhouettes of four species of *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa. A–C. *Elaphoglossum concinnum* Mickel. D–F. *Elaphoglossum bryogenes* Mickel. G–J. *Elaphoglossum rhomboideum* A. Vasco, Mickel & R. C. Moran. K–M. *Elaphoglossum deltoideum* (Sodiro) Christ. A from *Øllgaard & Fiel 91139* (AAU); B from *van der Werff & Palacios 9054* (NY); C from *Cottón et al. A1546* (NY); D from *Øllgaard et al. 35936* (AAU); E from *Luteyn & Sylva 14682* (MO); F from *Luteyn & Sylva 14682* (NY); G from *Holm-Neilsen et al. 6168* (UC); H from *Holm-Neilsen et al. 6168* (AAU); J from *Alston 8235* (MO); K from *Camp E-3419* (NY); L from *Sodiro s.n.* (K); M from *Sodiro s.n.* (P).







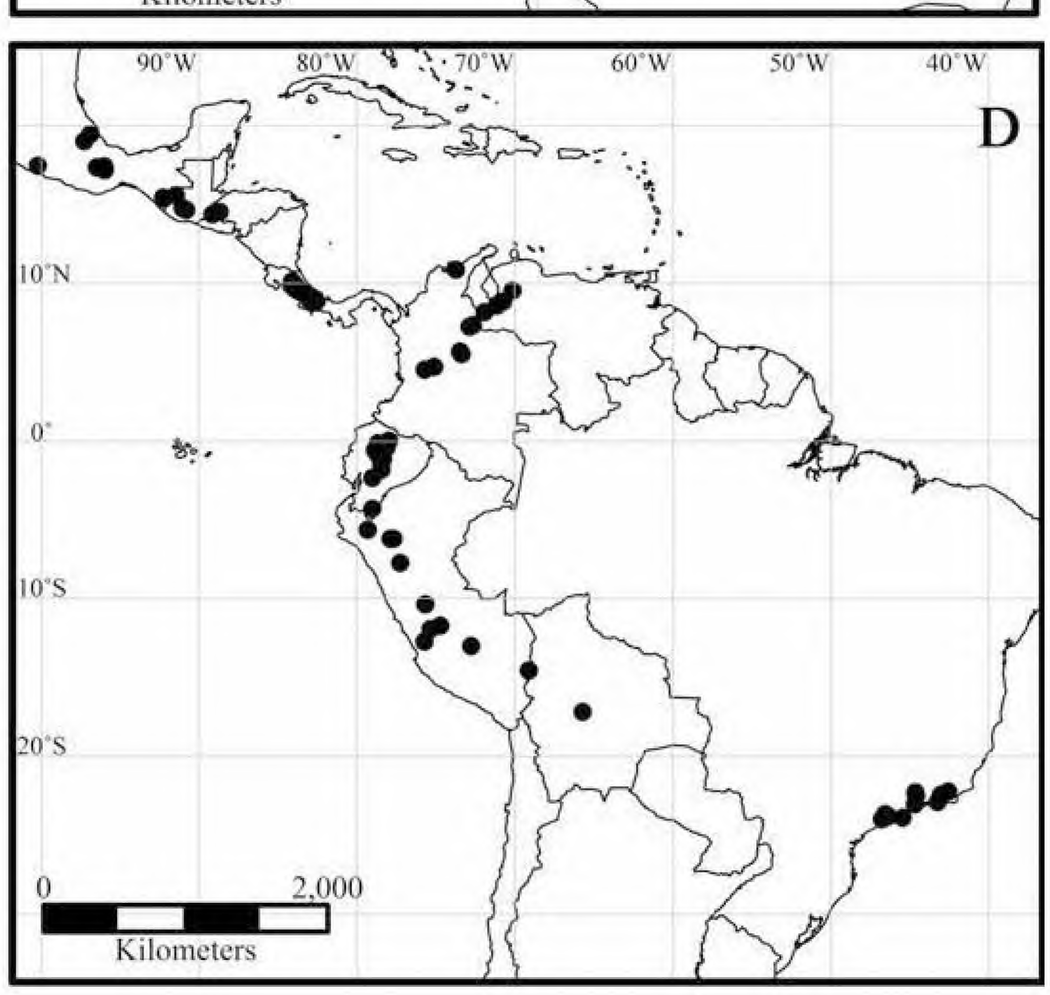


Figure 6. Distribution maps. —A. *Elaphoglossum blepharis* A. Vasco, Mickel & R. C. Moran (★), *E. deltoideum* (Sodiro) Christ (▲), and *E. moorei* (E. Britton) Christ (●). —B. *Elaphoglossum feei* (Bory ex Fée) T. Moore (▲) and *E. lloense* (Hook.) T. Moore (●). —C. *Elaphoglossum minutum* (Pohl ex Fée) T. Moore. —D. *Elaphoglossum squamipes* (Hook.) T. Moore.

Balslev 9530 (AAU, NY, QCA, UC). **Napo:** carr. Baeza–Quito, 5 km después de Cuyuja, hac. Flor del Bosque, *Navarrete 397* (AAU, NY, QCA, QCNE); Llanganati, N-facing slope toward Río Golpe, N of Chosa Aucacocha, *Øllgaard et al. 38623* (AAU, GH, UC). **Pichincha:** rd. Olmedo–laguna San Marcos, W of pass, *Øllgaard et al. 34364* (AAU). **Sucumbios:** cerro El Mirador, 4 km SW de la poblacion de Cocha Seca, subiendo por el sector de Chozas Viejas, *Gavilanes & Funk 848* (AAU, QCA).

2. Elaphoglossum anthracinum A. Vasco, Mickel & R. C. Moran, sp. nov. TYPE: Ecuador. Napo: 8–12 km ESE of Santa Barbara, 0°40′S, 77°30′W, 2780–2880 m, 11 Jan. 1985, *J. L. Luteyn & E. Cotton 11002* (holotype, QCA!; isotypes, MO!, NY! [3], QCNE!, UC!). Figures 1C, 3N–R, 4A–C.

Rhizomes 1 mm wide, long-creeping; rhizome scales 4–5 mm, appressed, lanceolate, entire, orange to brown, concolorous to darkened at point of attachment, lustrous. Sterile leaves 3–7 cm; petioles 0.8 to 2 times the lamina length; petiolar scales 1–2 mm, scattered, lanceolate, light orange to brown with black point of attachment, those scales toward petiole bases sometimes black proximally; laminae 1–2.5 × 1.2–2.2 cm, ca. as long as wide, coriaceous, simple, deltate, margins entire, apices rounded, bases truncate; adaxial lamina surface scaly, the scales 1.5–3 mm, scattered, straight to curved, linear to narrowly lanceolate, black, slightly hastate at the base; abaxial lamina surface scaly, the scales 2.5–3 mm, hastate, black, shiny. Fertile leaf (1 seen) 4.5 cm; petiole 3 times longer than laminae; lamina 1.2 × 1 cm, ovate, entire, apex broadly acute, base slightly cordate; intersporangial scales 2.5–3.2 mm, abundant, black, lustrous.

Etymology. *Elaphoglossum anthracinum* is distinguished by its many black lustrous laminar scales. This character gives rise to the specific epithet, which means "coal black" in Latin.

Distribution and elevation. *Elaphoglossum anthracinum* occurs in Colombia and Ecuador; specimens have been collected at elevations from 2780 to 3050 m.

IUCN Red List category. According to IUCN Red List criteria, at this point this species must be classified as DD (Data Deficient). Because *Elaphoglossum anthracinum* is a new species, more information is needed to determine its appropriate IUCN listing.

Discussion. *Elaphoglossum anthracinum* is distinguished by its deltate laminae, petiolar scales that are black around the point of attachment, and many black lustrous laminar scales. *Elaphoglossum anthracinum* resembles *E. andreanum* in the size of the leaves and the dark brown to black laminar scales. However, the new species differs by larger (2.5–3 mm vs. [0.2–]0.7–1.5 long in *E. andreanum*) scales on the abaxial surface of the laminae. The specimen with a single fertile leaf (*Lozano 3489*) has dense, black, shiny intersporangial scales 2.5–3 mm long; in contast, *E. andreanum* has intersporangial scales less dense, only 0.5–2 mm long, and ranging in color from light orange to dark brown or black.

Paratype. COLOMBIA. **Cauca:** Mpio. de Coconuco, valle de Paletará, Par. Nac. Nat. de Puracé, [2°12′15″N, 76°29′47″W], 3050 m, 29 July 1980, *G. Lozano 3489* (COL).

3. Elaphoglossum blepharis A. Vasco, Mickel & R. C. Moran, sp. nov. TYPE: Ecuador. Loja: Celica–Zapotillo rd., Km. 6–10, potreros and remnants of seasonal evergreen forest, [4°07′S, 79°59′W], 1800–1900 m, 10 Apr. 1980, *G. W. Harling & L. Andersson 18092* (holotype, AAU!). Figures 2A–D, 4D, E, 6A.

Rhizomes 1–2 mm wide, long-creeping; rhizome scales 3–4 mm, appressed, lanceolate, entire or with rare projections at base, orange-tan, dull. Sterile leaves 3–4.5 cm; petioles 0.8–1.5 times the lamina length; petiolar scales 1.5–3 mm, scattered to imbricate, narrowly lanceolate to ovate-lanceolate, mostly entire, light orange to brown, the base hastate or with projections; laminae 1–2 × 1.5–2 cm, ca. as long as wide, coriaceous, simple, deltate, margins entire, apices obtuse, bases truncate; adaxial lamina surface scaly, the scales 1–2 mm, linear, light orange to brown, concolorous, dull, the bases hastate by linear processes; abaxial surface scaly, the scales 0.3–1.2 mm, linear, with short inconspicous basal projections, orange, dull. Fertile leaves 7–10 cm; petioles 4 to 5.5 times the lamina length; laminae 1.2–2 × 0.7–1 cm, narrowly deltate, entire, apices obtuse, bases truncate to subcordate; intersporangial scales ca. 1 mm, scattered, narrowly lanceolate, hastate, light orange to brown, dull.

Etymology. *Elaphoglossum blepharis* has adaxial laminar scales that are hastate at the base by hairlike processes. This character gives rise to the specific epithet, which is a noun in apposition, meaning "eyelash" in Greek.

Distribution and elevation. As currently known, *Elaphoglossum blepharis* is restricted to Loja, Ecuador, collected at elevations from 1800 to 2200 m.

IUCN Red List category. According to IUCN Red List criteria, this species is classified as DD (Data Deficient). Because *Elaphoglossum blepharis* is a new species, more information is needed to determine its appropriate IUCN listing.

Discussion. *Elaphoglossum blepharis* differs from *E. andreanum* by its extremely narrow scales on the laminae adaxially. These scales are hastate with hairlike processes basally. Similar narrow scales are found on the laminae adaxially in *E. tripartitum*, which resolved as sister to *E. blepharis* in our chloroplast DNA sequence analyses (Vasco et al., in prep.). Furthermore, *E. blepharis* has laminae with entire margins, whereas those in *E. andreanum* are minutely crenulate.

Paratype. ECUADOR. **Loja:** Celica–Zapotillo Rd., ca. Km. 5, [4°07′S, 79°57′W], 2100–2200 m, 23 Feb. 1983, *G. W. Harling & L. Andersson 22455* (QCA).

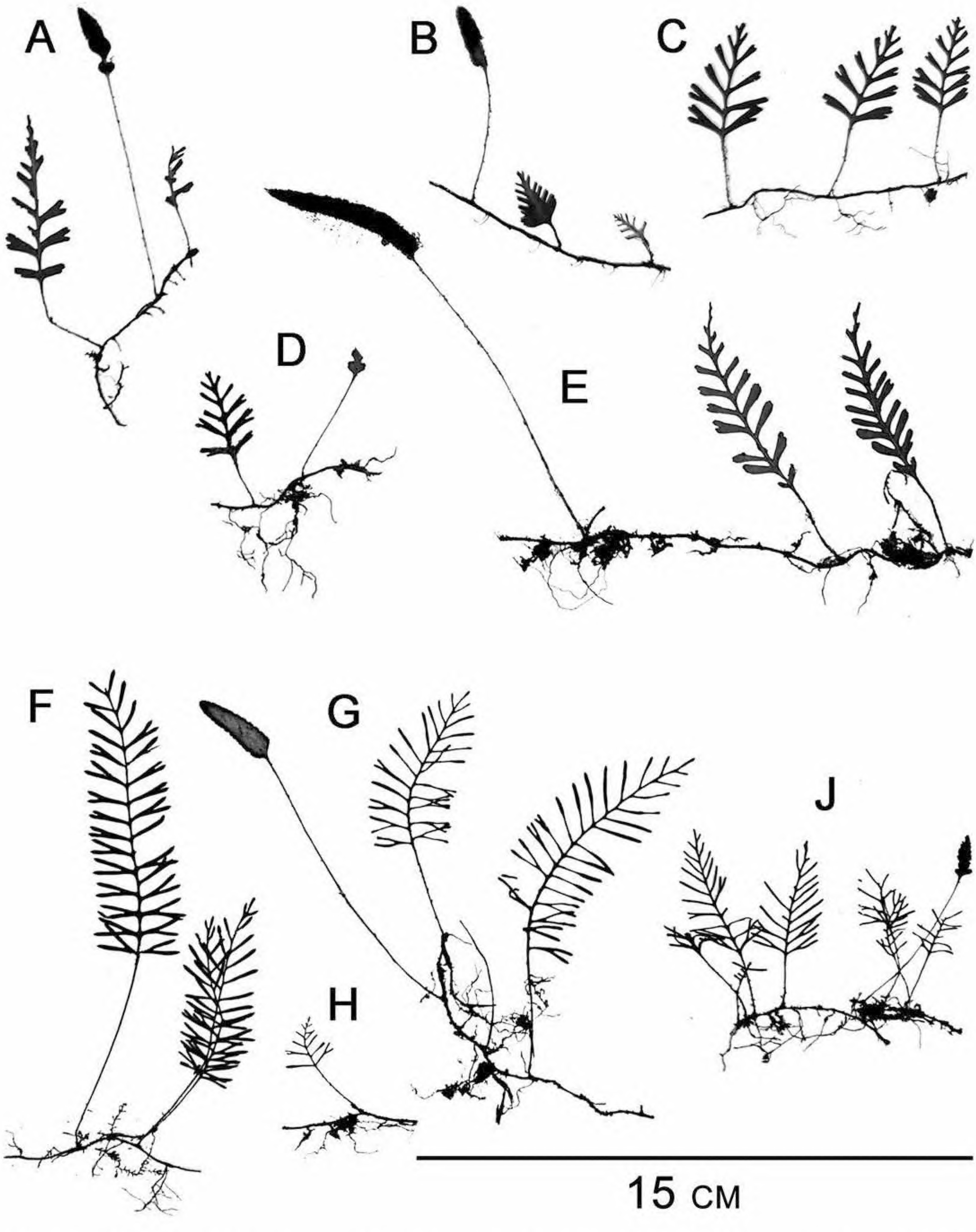


Figure 7. Silhouettes of the two species of *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa with pinnately divided laminae. A–E. *Elaphoglossum colombianum* (Maxon) Mickel. F–J. *Elaphoglossum moorei* (E. Britton) Christ. A from *van der Werff & Giraldo 9726* (NY); B from *Luteyn et al. 12248* (NY); C from *Ramos et al. 1139* (NY); D from *Vasco et al. 636* (NY); E from *van der Werff & Giraldo 9726* (NY); F from *Cayola et al. 2847* (MO); G, H from *Fernández & Altamirano 3110* (MO); J from *Kessler et al. 6961* (NY).

4. Elaphoglossum bryogenes Mickel, Brittonia 45: 213. 1993. TYPE: Ecuador. Napo: cordillera de Huacamayos, 4.3–16.5 km S of Cosanga on Baeza–Puyo rd., 0°37′S, 77°51′W, 1830–2130 m, 15 Oct. 1992, *J. L. Luteyn & D. S. Sylva 14682* (holotype, NY!; isotypes, AAU!, MO!, UC!, US!). Figures 1C, 2J–M, 5D–F.

Rhizomes 1 mm wide, long-creeping; rhizome scales 3–5 mm, appressed, lanceolate, entire, light

orange to brown, concolorous or dark at point of attachment, dull. Sterile leaves 2.1–3 cm; petioles 0.25 to 1.7 times the lamina length; petiolar scales 1–1.5 mm, scattered, lanceolate, entire, brown, concolorous, dull; laminae 1–1.8 × 0.4–0.7 cm, 0.8 to 1 times longer than wide, coriaceous, simple, narrowly rhombic, margins entire, apices rounded to broadly acute, bases short-cuneate; adaxial lamina surface scaly, the scales 1–2 mm, ovate to lanceolate, often hastate at the base, brown, slightly shiny; abaxial lamina surface scaly, the scales 1–1.5 mm, ovate to lanceolate, often hastate at the base, brown, slightly shiny. Fertile leaf (only 1 leaf seen) 3 cm; petiole 2 to 3 times longer than the lamina; lamina 1 × 0.6 cm, ovate to broadly elliptic, entire, apices broadly acute to rounded, bases broadly cuneate; intersporangial scales 1.5–2 mm, dark brown.

Distribution and elevation. *Elaphoglossum bryogenes* is known only from Ecuador, from the east side of the Andes, at elevations from 1800 to 2130 m.

Discussion. *Elaphoglossum bryogenes* greatly resembles *E. andreanum* in its laminar scales that are brown, ovate to lanceolate, and often hastate at the base. It differs by the entire and narrowly rhombic laminae, versus minutely crenulate and slightly elongated laminae in *E. andreanum*. Also, *E. bryogenes* generally has smaller leaves (2.3–3 cm vs. 2.6–9.5 cm long in *E. andreanum*).

Additional specimen examined. ECUADOR. **Napo:** rd. Baeza–Tena, ca. 23 km from Baeza, *Øllgaard et al. 35936* (AAU).

5. Elaphoglossum colombianum (Maxon) Mickel, Brittonia 32: 116. 1980, as "*columbianum*." Basionym: *Microstaphyla colombiana* Maxon, J. Wash. Acad. Sci. 13: 30. 1923. *Peltapteris colombiana* (Maxon) L. D. Gómez, Brenesia 6: 30. 1975. TYPE: Colombia. El Valle: La Cumbre, summit of W peak, [3°40′N, 76°35′W], 2100–2400 m, 11 & 18 Sep. 1922, *E. P. Killip 11365* (holotype, US!; isotypes, GH!, NY! [2]). Figures 1C, 7A–E, 8M, N.

Rhizomes 0.6–0.9 mm wide, long-creeping; rhizome scales 1–2.5 mm, appressed, lanceolate, subentire with occasional projections, light orange to brown, dull. Sterile leaves 3–17 cm; petioles 0.8 to 2.3 times the lamina length; petiolar scales 0.8–1.5 mm, scattered, clasping to spreading, ovate, with small marginal projections, light orange to brown; laminae 2.5–5.5 × 1.7–2.6 cm, 1 to 3.2 times longer than wide, chartaceous, pinnately divided, lanceolate to oblong or subtriangular, margins entire, apical segments similar to lateral ones, base truncate, cuneate or slightly reduced, pinnae 1–2 mm wide, 5 to 9 pairs, ascending, sometimes notched or divided at the apex; adaxial lamina surface glabrous to sparsely scaly, the scales 0.1–0.5 mm, brown, sometimes darker at point of attachment, dull; abaxial lamina surface sparsely scaly, the scales 0.1–1 mm, with small marginal projections, brown, sometimes darker at point of attachment. Fertile leaves 4–14 cm long; petioles 2.1 to 5.5 times the lamina length; laminae 0.9–4.5 × 0.3–1 cm, oblong, entire to shallowly lobed, rarely with 1 free pair of proximal pinnae, apices rounded, bases truncate; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum colombianum* is known only from western Colombia at elevations from 1600 to 2400 m.

Discussion. *Elaphoglossum colombianum* resembles *E. moorei* in its pinnately divided laminae, but differs by fewer and wider pinna pairs. There are five to nine pinna pairs that extend to 2 mm wide at their bases in *E. colombianum*, which contrasts with eight to 17 pinna pairs that are 0.4–1 mm wide at their bases in *E. moorei* (also see Fig. 7). Pinnae in *E. colombianum* tend to be more ascending compared to those of *E. moorei*. The two species are distinct geographically: *E. colombianum* is restricted to western Colombia (Fig. 1C), whereas *E. moorei* is restricted to Peru and Bolivia (Fig. 6A).

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Yarumal/Valdivia, vereda El Cedro, sitio Alto de Ventanas, *Gómez et al. 685* (HUA). **Chocó:** Mpio. San José del Palmar, cerro del Torrá, vertiente W del río Negro abajo del Helipuerto, vereda del río Negro, *Ramos-Pérez et al. 1063* (NY), *Ramos-Pérez et al. 1103* (NY), *Ramos-Pérez et al. 1139* (NY). **Risaralda:** Mpio. Pueblo Rico, vereda Montebello, cerca a Los Cajones, subiendo hacia la base militar, *Vasco et al. 622* (HUA, NY), *Vasco et al. 636* (HUA, NY). **Valle del Cauca:** Mpio. El Cairo, Serranía de Los Paraguas, Valle-Chocó border, *Luteyn et al. 12248* (NY); Mpio. Cali, finca Zingara, at Km. 18 rd. Cali–Buenaventura, *van der Werff & Giraldo 9726* (MO, NY, PMA, UC).

6. Elaphoglossum concinnum Mickel, Fieldiana, Bot., n.s. 27: 128. 1991. TYPE: Peru. San Martín: Prov. Mariscal Cáceres, Río Abiseo Nat. Park, near Las Papayas ruins, 7°56′S, 77°21′W, 2600–2850 m, 26 July 1985, *K. R. Young 1301* (holotype, NY!). Figures 1C, 2R–U, 3G–L, 5A–C.

Rhizomes 0.5–1 mm wide, long-creeping; rhizome scales 4–7 mm, appressed, narrowly lanceolate, entire, orange-tan, dull. Sterile leaves 0.9–2.6(–3.5) cm; petioles 1.2 to 3 times the lamina length; petiolar scales 1–2.5 mm, scattered, spreading, lanceolate to

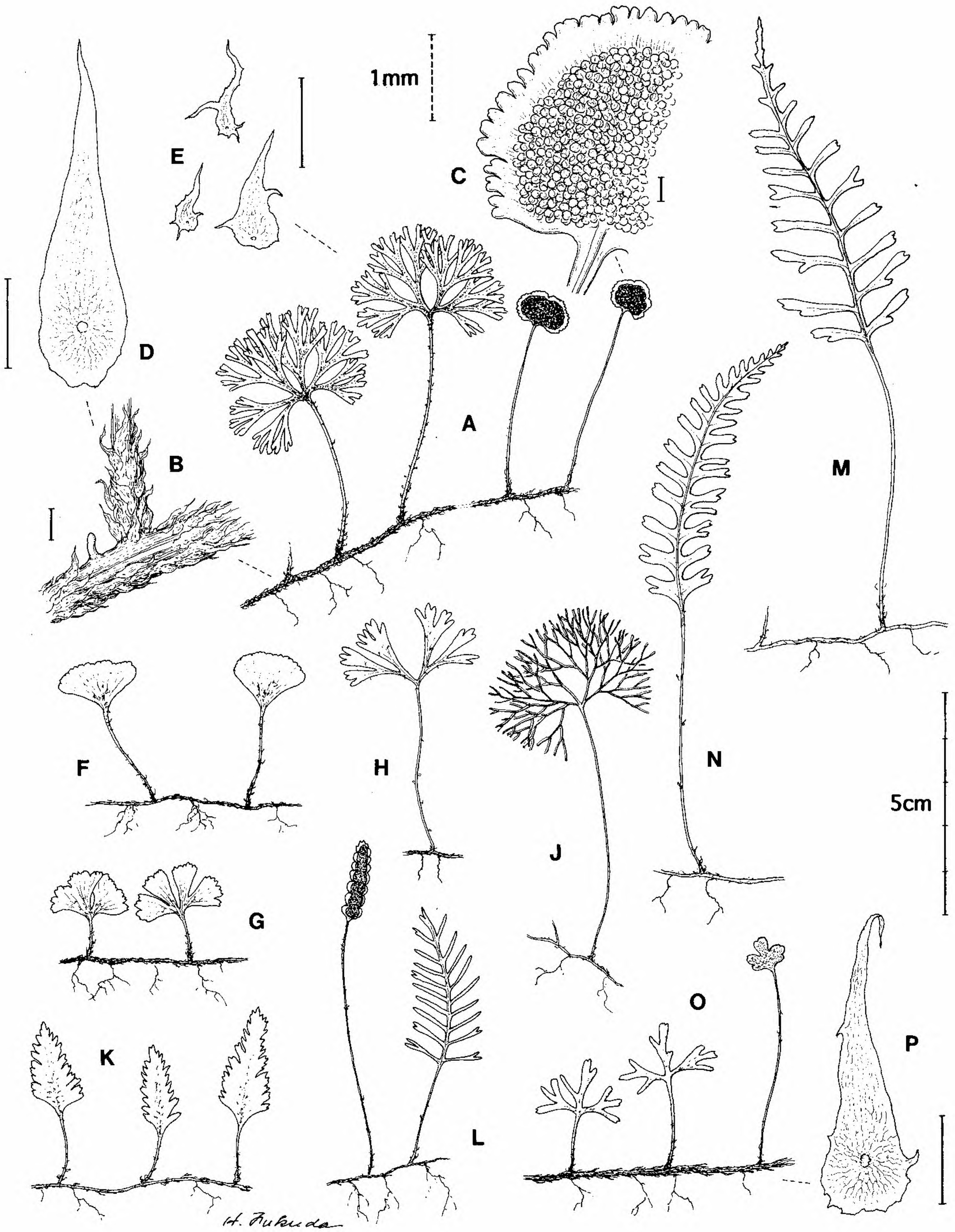


Figure 8. A–E. *Elaphoglossum peltatum* (Sw.) Urb. f. *peltatum*. —A. Habit, with two fertile leaves at right. —B. Rhizome detail, note peglike aerophore at left of petiole base. —C. Fertile lamina detail. —D. Rhizome scale. —E. Laminar scales. —F. *Elaphoglossum peltatum* f. *standleyi* (Maxon) Mickel, habit, sterile leaves only. G, H. *Elaphoglossum peltatum* f. *flabellatum* (Humb. & Bonpl. ex Willd.) Mickel. —G. Habit, sterile leaves only, dichotomously divided. —H. Habit, sterile leaf only, showing greater division of dichotomous lobing of lamina. —J. *Elaphoglossum peltatum* (Sw.) Urb. f. *peltatum*, habit. —K. *Elaphoglossum moorei* (E. Britton) Christ × unknown hybrid parent, sterile leaves, showing the lack of pinnate division to laminae. —L. *Elaphoglossum moorei* (E. Britton) Christ, habit, fertile leaf at left, sterile leaf at right with typical pinnate division. M, N. *Elaphoglossum colombianum* (Maxon) Mickel, sterile leaves. O, P. *Elaphoglossum tripartitum* (Hook. & Grev.)

hastate, entire, orange to brown; laminae 0.4–1.2 × 0.5–0.9 cm, 1.3 to 2.5 times longer than wide, subcoriaceous, simple, ovate and suborbicular to rhombic, margins entire, apices obtuse, bases shortly decurrent along petiole; adaxial lamina surface glabrous to sparsely scaly, the scales 1–2 mm, narrowly lanceolate, dark brown to black but lighter than those on the abaxial surface, slightly shiny; abaxial lamina surface sparsely scaly, the scales 1–2 mm, linear to deltate, subentire, with sparse irregular teeth, dark brown to black, sometimes with brown borders. Fertile leaves 4–7 cm; petioles 4 to 5 times the lamina length; laminae 0.7–1.5 × 0.5–1.6 cm, ovate to suborbicular, entire, apices obtuse, bases truncate to slightly cordate; intersporangial scales 1–2 mm, scattered, hastate, dark reddish brown to black, shiny.

Distribution and elevation. *Elaphoglossum concinnum* is found in southern Ecuador and northern Peru, at elevations from 2450 to 3000 m.

Discussion. *Elaphoglossum concinnum* is characterized by suborbicular to ovate or rhombic laminae with obtuse apices. *Elaphoglossum andreanum* is similar, but differs by the typically slightly elongate deltate laminae with minutely crenulate margins. See *E. rhomboideum* for a comparision with that species.

Additional specimens examined. ECUADOR. **Loja:** Rd. Loja–Saraguro, Km. 28, *Cotton et al. A1546* (MO, NY, QCA, QCNE); am Ramos-Urca und Cerro Acacana, *Lehmann 7658* (K); new rd. Loja–Saraguro, Km. 17, *Øllgaard & Feil 91139* (AAU, QCA, QCNE); about 10 km SW of Loja, along rd. past the university towards La Violeta, *van der Werff & Palacios 9054* (MO, NY, QCNE, UC). **Zamora-Chinchipe:** new rd. Loja–Zamora, ca. 4 km E of pass "El Tiro," *Lehnert 1409* (NY, UC).

PERU. **Amazonas:** ridge above the small settlement "quebrada Oso Perdido," on carretera marginal betw. Pedro Ruiz & Moyobamba, *Pimelkese 1367* (MO).

7. Elaphoglossum deltoideum (Sodiro) Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36: 56, fig. 19. 1899. Basionym: *Acrostichum deltoideum* Sodiro, Crypt. Vasc. Quit. 466. 1893. TYPE: Ecuador. Chimborazo: "la pendiente occidental del Chimborazo, cerca de Tamboloma," [1°28′S, 78°49′W], s.d., *A. Sodiro s.n.* (holotype, P!, P photo MO; isotype, K!). Figures 3M, 5K–M, 6A.

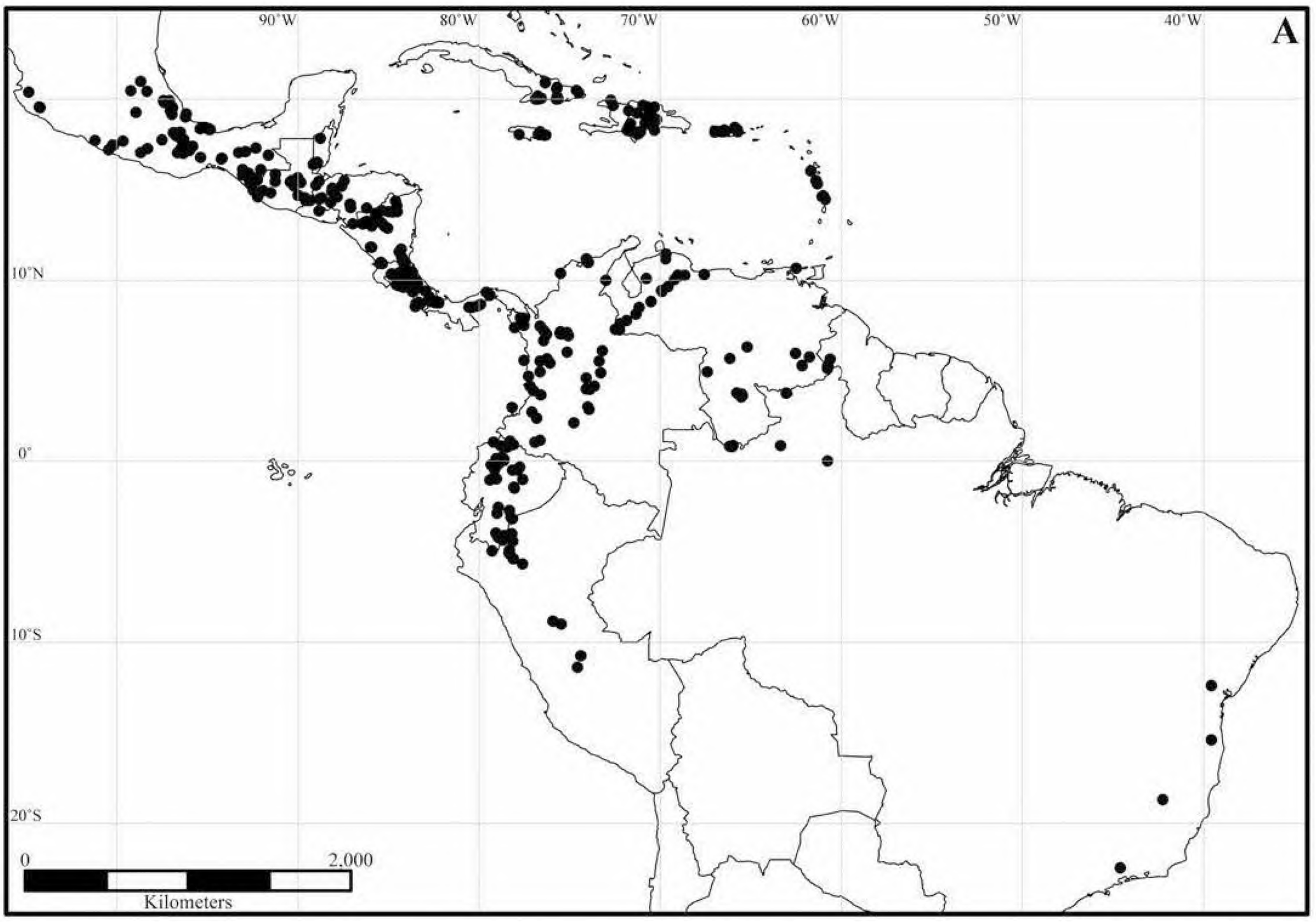
Rhizomes 1–2 mm wide, long-creeping; rhizome scales 5–6 mm, appressed, lanceolate, entire or with occasional projections, light orange to brown, dull. Sterile leaves 3.4–6 cm; petioles 0.8 to 2.5(to 4) times the lamina length; petiolar scales 1–2 mm, scattered, lanceolate, hastate, entire, brown, concolorous or dark at point of attachment; laminae 1–2.5 × 1.5–2 cm, ca. as long as wide, chartaceous, simple, deltate or sometimes slightly hastate, margins usually crenulate, apices acute, bases truncate; adaxial lamina surface sparsely scaly, the scales 0.4–1.5 mm, linear-hastate (the body only 2 or 3 cells wide), brown to light brown; abaxial lamina surface sparsely scaly, the scales 0.5–1.5 mm, laceolate to hastate, light brown to brown. Fertile leaves 5–6 cm, petioles 2 to 4 times the lamina length; laminae 1.2–2 × 0.7–0.9 cm, ovate to deltate, apices obtuse, bases truncate to cuneate; intersporangial scales 1.5–2 mm, filiform-hastate, brown.

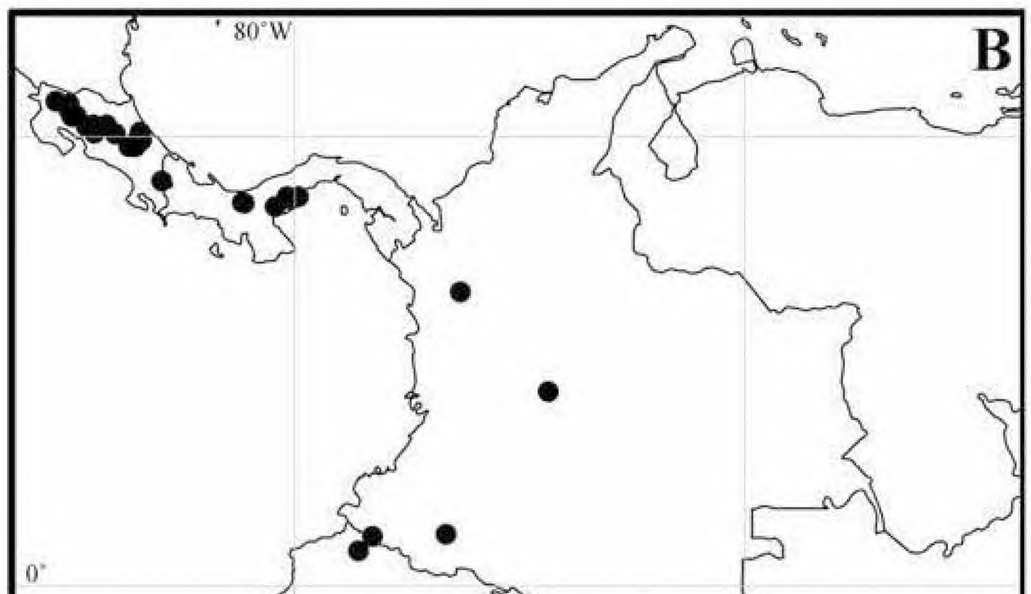
Distribution and elevation. *Elaphoglossum deltoideum* is known only from Volcan Cotopaxi and Chimborazo in Ecuador, at elevations from 1600 to 2400 m.

Discussion. *Elaphoglossum deltoideum* is distinguished by broadly deltate laminae that are sometimes hastate. One collection (*Croat 73680*) is atypical in its thinner laminae and some more elongate leaves as in *E. andreanum*; otherwise, the collection seems typical for *E. deltoideum*.

Elaphoglossum deltoideum sometimes exhibits laminae that are slightly hastate or 3-lobed (Fig. 3M), and in these lobes it approaches *E. tripartitum*, which has much more finely divided leaves. Nevertheless, a few specimens of *E. tripartitum* (e.g., *Holm-Nielsen 18151*, *Laegaard 54626*) have typical leaves mixed with some that are less divided. These less-divided laminae are indistinguishable from the hastate or 3-lobed individual laminae of *E. deltoideum*. This observation suggests that the two species are related; in fact, a sister relationship between the two species is supported by molecular phylogenetic studies of chloroplast DNA sequences (Vasco et al., in prep.).

←
Mickel. —O. Habit, with three leaves, fertile one at right. —P. Rhizome scale. A–E from *Méndez 7931* (NY); F from *Asplund 19710* (NY); G from *Luteyn 10765* (NY); H from *Øllgaard 98068* (AAU); J from *Holm-Nielsen et al. 2944* (MO); K from *Kessler 7078* (NY); L from holotype *Bang 558* (NY); M, N from isotype *Killip 11365* (NY); O from *Jameson 44* (NY). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.





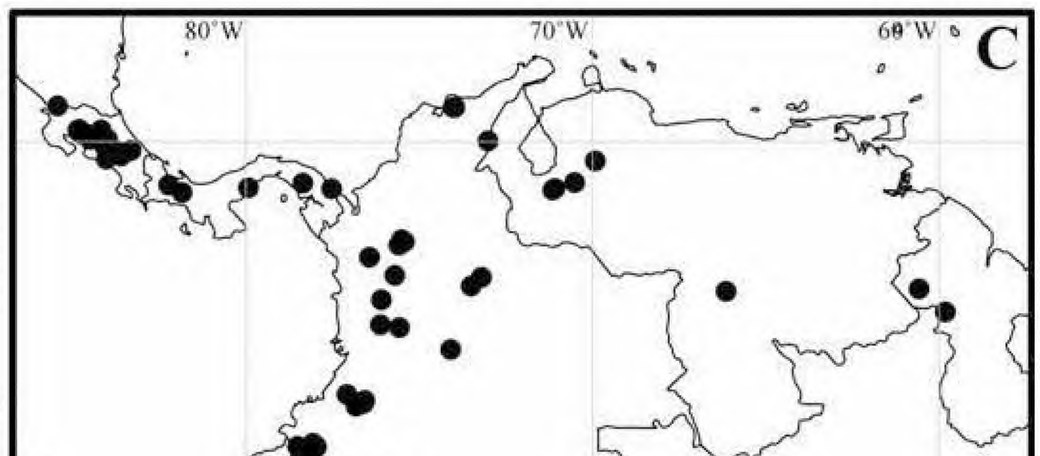


Figure 9. Distribution maps. —A. *Elaphoglossum peltatum* (Sw.) Urb. f. *peltatum*. —B. *Elaphoglossum nidiforme* Mickel (★) and *E. peltatum* f. *standleyi* (Maxon) Mickel (●). —C. *Elaphoglossum peltatum* f. *flabellatum* (Humb. & Bonpl. ex Willd.) Mickel.

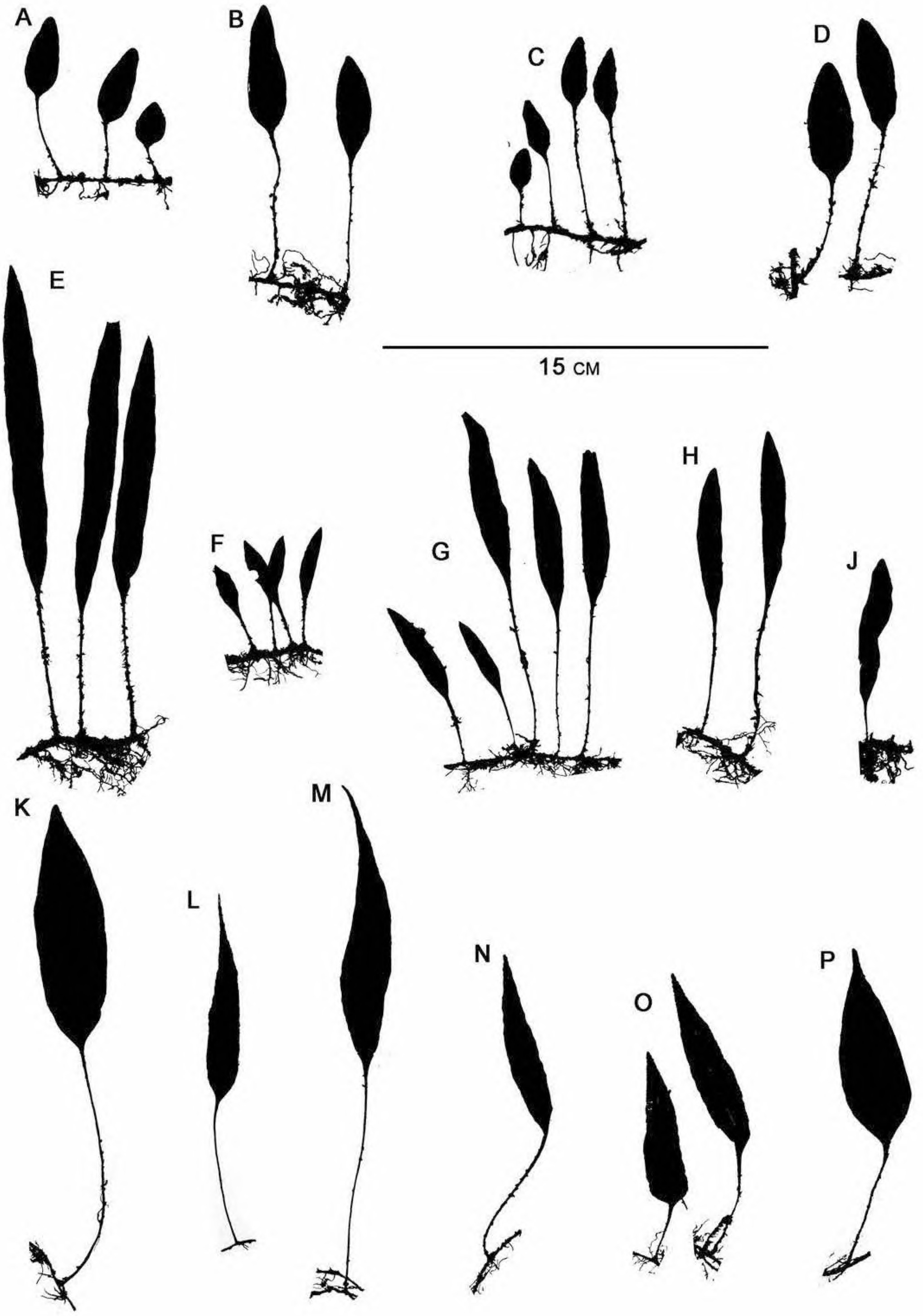


Figure 10. Silhouettes of three species of *Elaphoglossum* sect. *Squamipedia* Mickel & Atehortúa. A–D. *Elaphoglossum squamipes* (Hook.) T. Moore. E–J. *Elaphoglossum minutum* (Pohl ex Fée) T. Moore. K–P. *Elaphoglossum lloense* (Hook.) T. Moore. A from *Brade & Tamandaré 6447* (NY); B from *Bang 1791* (NY); C from *Davidse et al. 25834* (MO); D from *Rojas & Alfaro 4662* (MO); E from *Kessler et al. 8300* (NY); F from *Martínez-Salas & Stevenson 23981* (NY); G from *Moran et al. 6206* (NY); H from *Proctor 22170* (NY); J from *Mickel 7326* (NY); K from *Franco et al. 2883* (MO); L from *Dorr & Barnett 8249* (NY); M from *Hagemann 660* (COL); N from *Núñez 404* (MO); O from *Holm-Nielsen et al. 5657* (AAU); P from *Núñez 51* (MO).

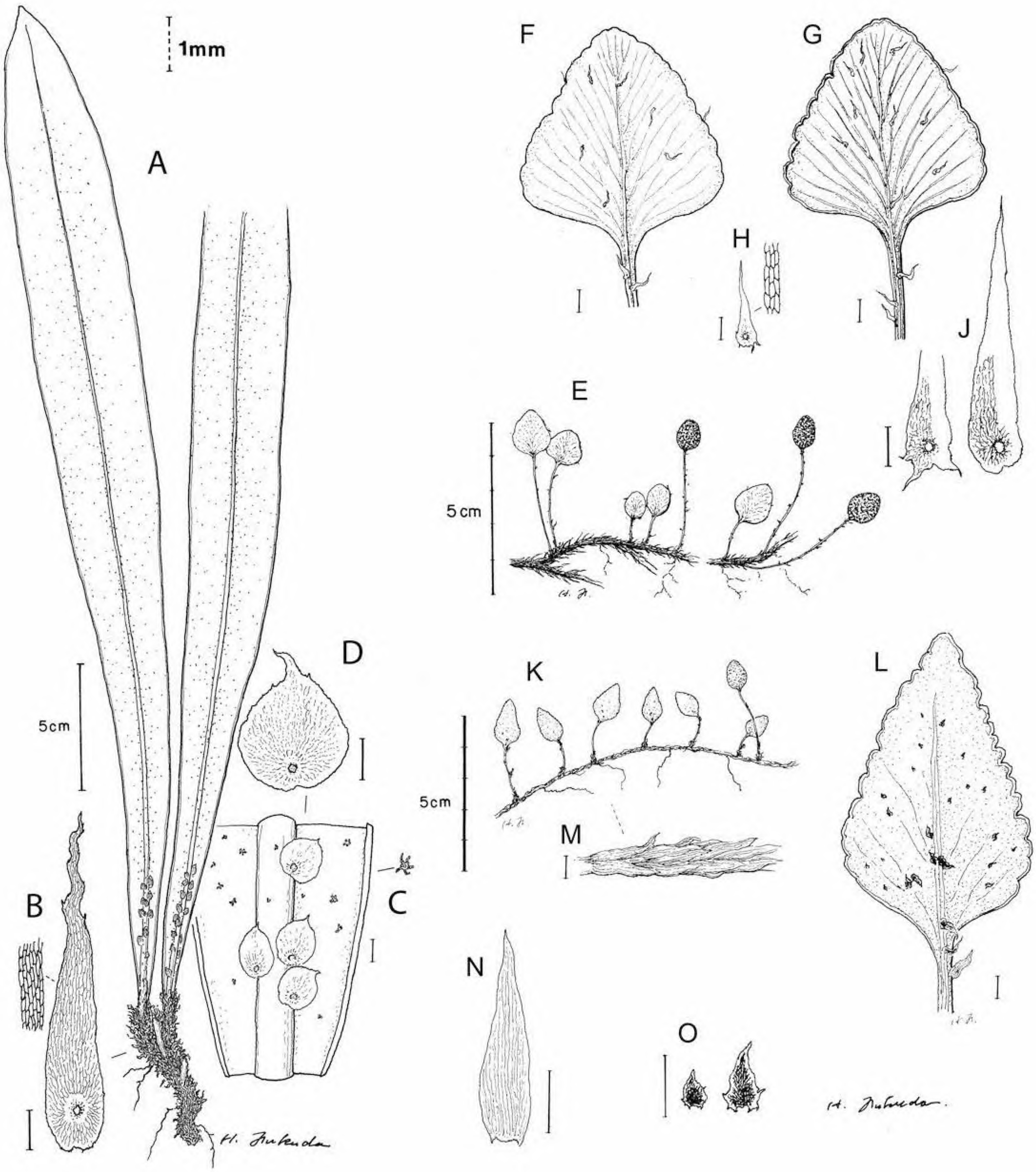


Figure 11. A–D. *Elaphoglossum nidiforme* Mickel. —A. Habit. —B. Rhizome scale. —C. Base of sterile lamina, abaxial surface, with detail of microscale at right. —D. Rachis scale from abaxial surface of costa. E–J. *Elaphoglossum rhomboideum* A. Vasco, Mickel & R. C. Moran. —E. Habit, showing three dimorphic and taller fertile leaves to right. —F. Adaxial lamina. —G. Abaxial lamina. —H. Petiolar scale. —J. Rhizome scales. K–O. *Elaphoglossum andreanum* Christ. —K. Habit, with one fertile leaf at right. —L. Abaxial lamina. —M. Rhizome. —N. Rhizome scale. —O. Abaxial laminar scales. A–D from *Lehnert & Kessler 1316* (NY); E–J from *Alston 8235* (MO); K–O from *André 3114* (NY). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.

Additional specimens examined. ECUADOR. **Chimborazo:** ca. 5 km N of Huigra, Cañon of Río Chanchan, *Camp E-3419* (NY). **Cotopaxi:** Cantón Pujilí, along rd. betw. El Corazón & Angamarca, along side rd. to Yasaucho, 0.3–0.4 km off of main rd., 3.1 km above main square in El Corazón, *Croat 73680* (MO, QCNE); around Pilalo, *Holm-Nielsen & Jeppesen 1365* (AAU, GH).

8. Elaphoglossum feei (Bory ex Fée) T. Moore, Index Fil. 16: 356. 1857. Basionym: *Acrostichum feei* Bory ex Fée, Mém. Foug. 2: 48, tab. 18, fig. 2. 1845. TYPE: Guadeloupe. Near bains chauds de Matouba, [16°02′N, 61°41′W], 1844, *de Thiouville s.n.* (holotype, P!, P photos GH!, US!). Figures 6B, 15D, E.

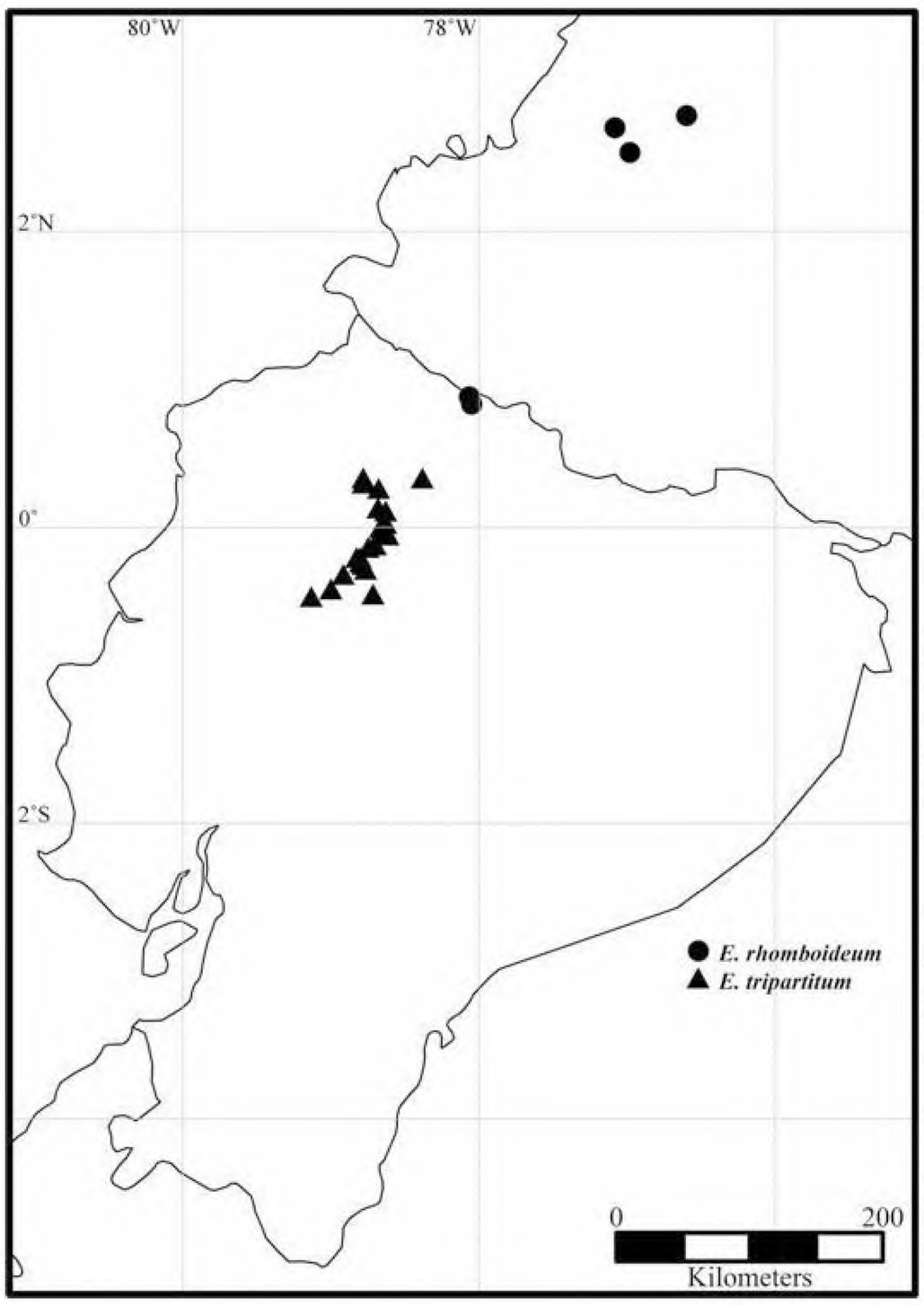


Figure 12. Distribution map of *Elaphoglossum rhomboideum* A. Vasco, Mickel & R. C. Moran (●) and *E. tripartitum* (Hook. & Grev.) Mickel (▲).

Rhizomes 0.6–1 mm wide, long-creeping; rhizome scales 1.4–2.8 mm, appressed, lanceolate, entire, light orange to brown, dull. Sterile leaves 3–9.5 cm; petioles 0.2 to 0.5 times the lamina length; petiolar scales 1–2 mm, scattered, lanceolate, entire, brown, concolorous; laminae 2–6 × 0.3–0.8 cm, 3.8 to 9.1 times longer than wide, chartaceous, simple, narrowly elliptical, margins crenulate, apices acute to obtuse, bases narrowly cuneate, often decurrent to the petiole base; adaxial lamina surface glabrous; abaxial lamina surface with scattered scales, the scales 0.2–0.5 mm, stellate to laceolate, orange to light brown, dull. Fertile leaves 4–8.5 cm; petioles 2.5 to 4 times the lamina length; laminae 0.8–2 × 0.2–0.5 cm, narrowly elliptic to lanceolate, entire to faintly crenulate, apices acute to rounded, bases cuneate; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum feei* is found in Guadeloupe and Dominica, at elevations from 750 to 1200 m.

Discussion. *Elaphoglossum feei* is characterized by short petioles, narrowly elliptic laminae with crenulate margins, and laminae that are 3–8 mm wide. The abaxial laminar scales are entire, lacking the basal projections on the margins that are present in other species of *Elaphoglossum* sect. *Squamipedia*. Superficially, *E. feei* resembles *E. wrightii*, a Cuban endemic originally placed in *Elaphoglossum* subsect. *Feeana* Christ [in *Elaphoglossum* sect. *Squamipedia*] by Mickel and Atehortúa (1980). *Elaphoglossum wrightii* differs from *E. feei* by larger and widely elliptic or oblanceolate laminae (Fig. 15F–J). *Elaphoglossum wrightii* is here excluded from *Elaphoglossum* sect. *Squamipedia* on the basis of chloroplast sequence data (Vasco et al., in prep.; see Excluded Species).

Additional specimens examined. DOMINICA. Mt. Anglais, *Hodge 22* (NY); Mt. Diablotin, *Hodge 2790* (GH, NY); Morne Anglais, *Hodge 2297* (GH, NY); pont Cassè, part way up Mt. Trois Pitons, *Lellinger 633* (US); Laudat, *Lloyd 150* (NY); Mt. Diablotin, *Lloyd 890* (NY); Mt. Diablotin, NW ridge, *Webster 13340* (GH, US).

GUADELOUPE. Matouba, Arins Chauds, ravine a Dejeuner, *Duss 4135* (F, GH, MO, NY); 1862, *L'Herminier s.n.* (GH, NY, US); bains-Jaunet, savane aux ananas, *Stehlé 1791* (NY, US).

9. Elaphoglossum lloense (Hook.) T. Moore, Index Fil. 11: 360. 1857. Basionym: *Acrostichum lloense* Hook., Icon. Pl. tab. 657. 1844. TYPE: Ecuador. Pichincha: valley of Lloa, [0°15′S, 78°35′W], *W. Jameson s.n.* (holotype, K!; isotype, P!, P photo F!). Figures 3S, T, 6B, 10K–P, 14.

Elaphoglossum ensiforme Mickel, Fieldiana, Bot., n.s. 27: 131. 1991. TYPE: Peru. Cuzco: Urubamba, Machu Picchu, Liactapampa, below Palcay on Aobamba river, [13°09′S, 72°31′W], 3300 m, 7 July 1982, *S. Peyton & T. Peyton 814* (holotype, MO!, MO photo NY!).

Elaphoglossum rhynchophyllum Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36: 57, fig. 20. 1899. TYPE: Venezuela. Mérida: [8°51′S, 70°44′W], 1889, *Engel 118* (holotype, P!).

Elaphoglossum serpentinum A. Rojas & W. D. Rodríguez, Actual. Biol. 34: 178. 2012. TYPE: Colombia. Antioquia: Municipio de Ituango, Km. 12.5 of rd. La Granja–Santa Rita de Ituango, 7°12′N, 75°42′W, 1930 m, 12 May 1988, *J. Zarucchi & J. Betancur 6484* (holotype, HUA!; isotype, MO).

Elaphoglossum teleglottis Mickel, Novon 2: 381. 1992. TYPE: Panama. Chiriquí: Distrito Bugaba, Cerro Punta, around STRI house, 8°51′S, 70°44′W, 2200 m, 27 Jan. 1984, *H. van der Werff & J. Herrera 6503* (holotype, NY!; isotypes, MO!, UC!).

Rhizomes 1–2 mm wide, long-creeping; rhizome scales 2–5 mm, appressed, ovate to narrowly lanceolate, irregularly and minutely toothed, light orange to dark brown, concolorous to darkened medially with broad lustrous dark brown to black central streak, dull. Sterile leaves 6–25 cm; petioles

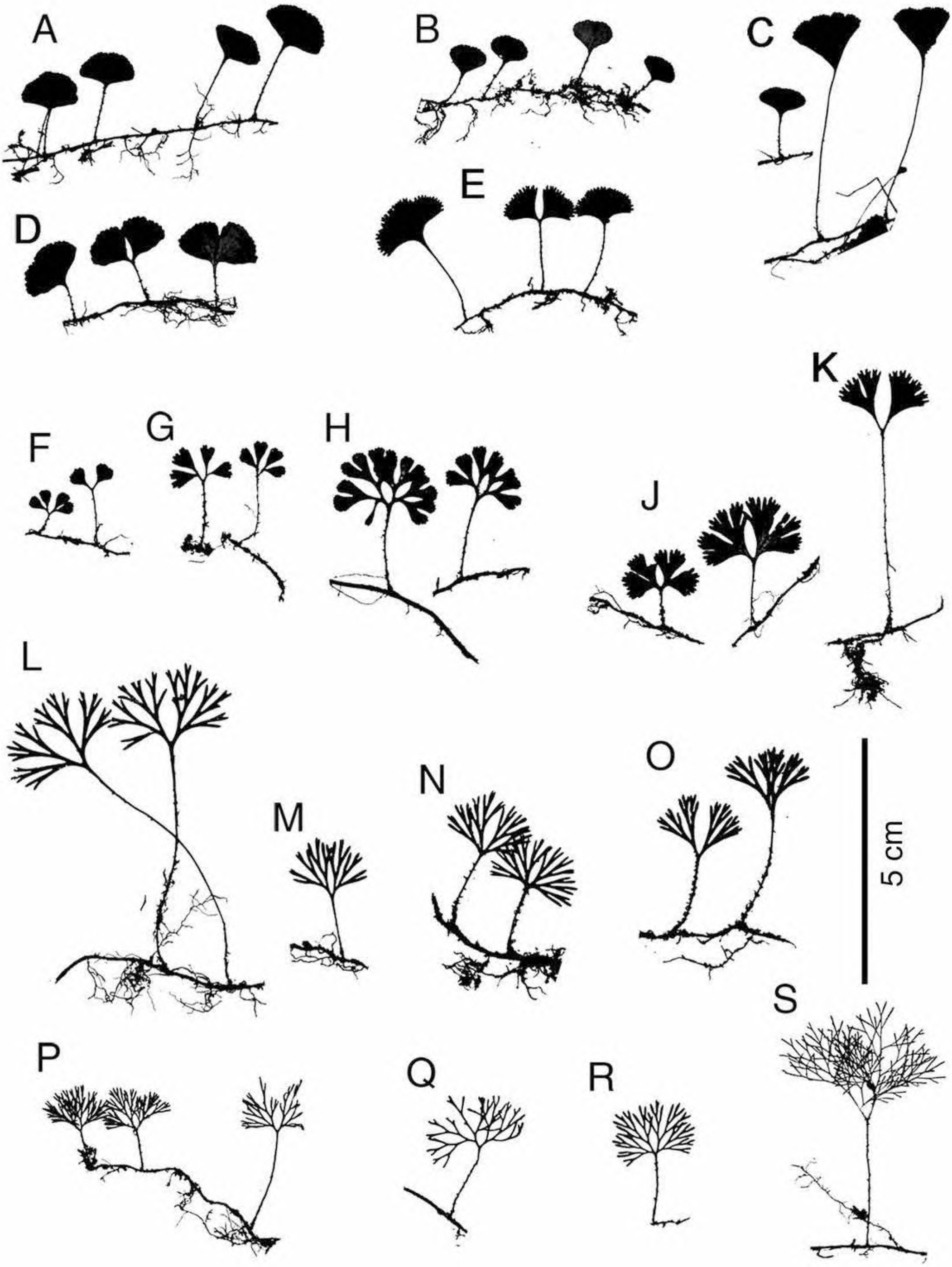


Figure 13. Silhouettes of the three forms of *Elaphoglossum peltatum* (Sw.) Urb. A–C. *Elaphoglossum pelatum* f. *standleyi* (Maxon) Mickel. D–K. *Elaphoglossum peltatum* f. *flabellatum* (Humb. & Bonpl. ex Willd.) Mickel. L–S. *Elaphoglossum peltatum* (Sw.) Urb. f. *peltatum*. A from *Fay & Fay 3604* (NY); B from *Wagner 78631* (NY); C from *Øllgaard et al. 35600* (AUU); D from *Folsom et al. 6677* (AAU); E from *Steyermark et al. 126785* (MO); F from *Churchill et al. 4839* (MO); G from *McPherson 9529* (MO); H from *Alfaro 523* (NY); J from *Correa et al. 8586* (NY); K from *Ortega & van der Werff 2356* (MO); L from *Gastony et al. 240* (NY); M from *Barbor s.n.* (NY); N from *Giraldo-Cañas 379* (MO); O from *Mickel 8884* (NY); P from *Luteyn et al. 10693* (NY); Q from *Smith et al. 5959* (MO); R from *Croat & Watt 70389* (MO); S from *Laegaard 51596B* (AAU).

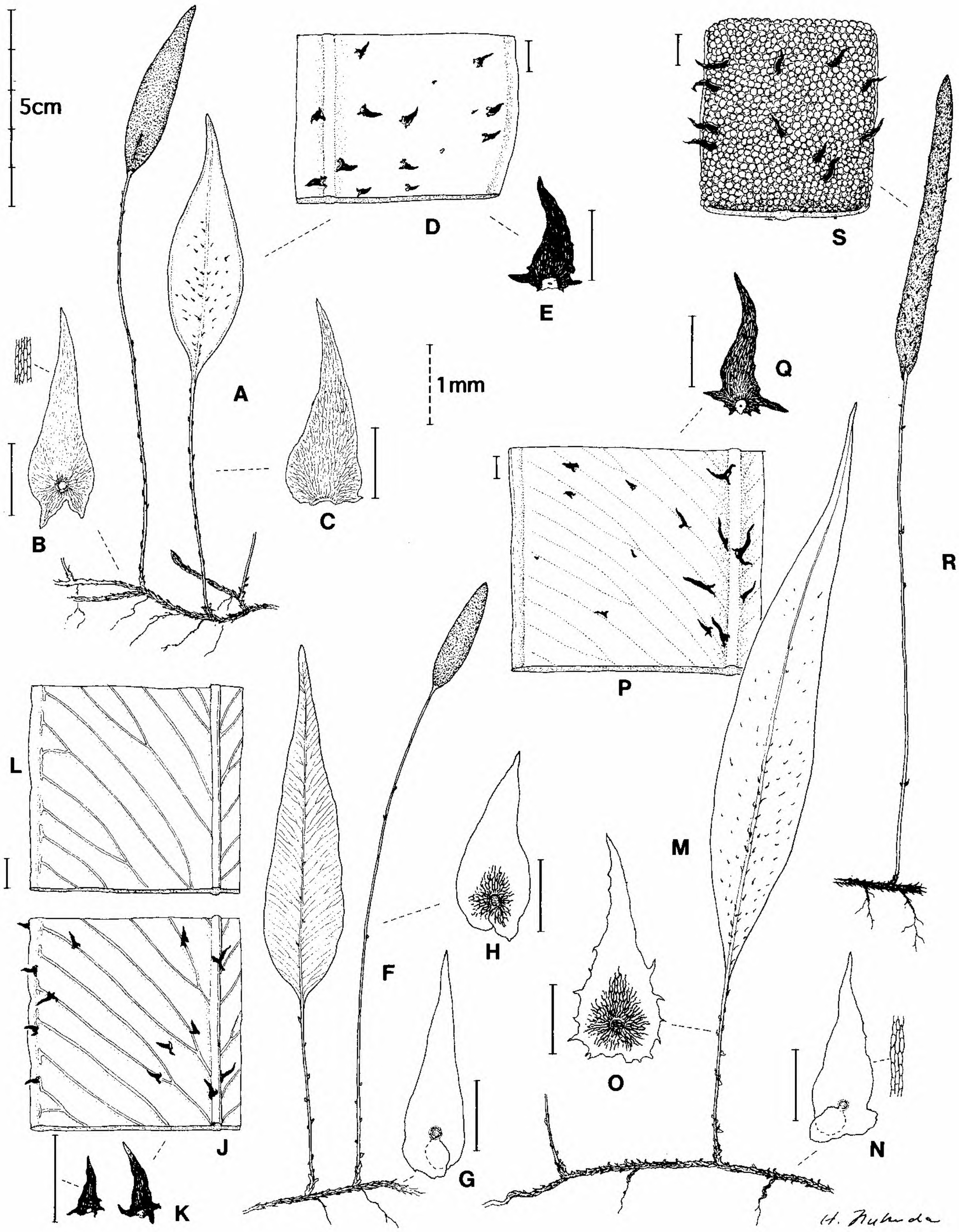


Figure 14. A–S. *Elaphoglossum lloense* (Hook.) T. Moore showing differences in sterile leaf shapes and sizes. —A. Habit, with fertile leaf at left. —B. Rhizome scale. —C. Petiolar scale. —D. Adaxial lamina detail. —E. Laminar scale. —F. Habit, with fertile leaf at right. —G. Rhizome scale. —H. Petiolar scale. —J. Abaxial lamina detail. —K. Abaxial laminar scales. —L. Adaxial lamina detail. —M. Habit. —N. Rhizome scale. —O. Petiolar scale. —P. Abaxial lamina detail. —Q. Abaxial laminar scale. —R. Fertile leaf. —S. Fertile lamina detail. A–E from *Sodiro s.n.* (AAU); F–L from *Dorr et al. 7301* (NY); M–Q from *Navarrete & Asimbaya 1644* (NY); R, S from *Steyermark & Liesner 118353* (NY). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.

0.5 to 2.5 times the lamina length; petiolar scales 1.5–4 mm, scattered, ovate to ovate-attenuate, entire, brown, concolorous or darkened at point of attachment; laminae 2–15 × 1.1–2.8(–4) cm, (2 to)3 to 14 times longer than wide, chartaceous, simple, lanceolate to narrowly elliptic, margins entire or (especially small laminae) minutely crenulate, apices attenuate, acute to acuminate, bases cuneate to rounded; adaxial lamina surface scaly, the scales (0.3–)1–2.5 mm, minute and circular to large and narrowly lanceolate, light brown to black, dull or shiny, the apices attenuate, irregularly toothed or with occasional processes, sometimes hastate; abaxial lamina surface scaly, the scales (0.3–)1–2 mm, like those adaxially. Fertile leaves 7–27.5 cm; petioles 2.2 to 4.3 times the lamina length; laminae 1.5–7.5 × 0.5–1.2 cm, ovate to narrowly lanceolate, entire, apices acuminate to attenuate, bases cuneate to long-tapering; intersporangial scales absent or if present 1–2 mm, narrowly lanceolate, toothed or with lateral processes, brown to black.

Distribution and elevation. *Elaphoglossum lloense* is epiphytic in wet forests of Bolivia, Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela; specimens have been collected at elevations of (350–)900–3700 m.

Discussion. Compared to other species in the section, *Elaphoglossum lloense* has larger sterile leaves that are 6–25 cm long and 1.1–2.8(–4) cm wide, often with acute or long-attenuate apices. The latter (apex) character will often serve to distinguish the species from those with a similar general leaf shape, such as *E. minutum* (Pohl ex Fée) T. Moore and *E. squamipes* (Fig. 10). Nevertheless, *E. lloense* varies greatly in size and shape of the laminae, especially in lamina width and the angle of tapering toward the base (Fig. 14). Small leaves (< 3 cm long) appear quite different from larger ones, often with laminae elongate to deltate, minutely crenulate, and abruptly contracted and decurrent at the base (Fig. 2E–H). Such leaves greatly resemble those of small species (e.g., *E. andreanum*), but can generally be distinguished by the thinner texture with more evident venation in *E. lloense*. The laminar scales are also extremely variable in color and shape, varying from pale brown to black, and minute and circular to large and hastate. Although quite distinct, these extremes intergrade and can sometimes be found on the same plant. Specimens from Costa Rica and Panama with narrow, hastate pale brown scales have been recognized as *E. teleglottis*, but these appear to be part of the variation within the species and are greatly similar to Andean plants. Molecular phylogenetic analyses using sequence data from three chloroplast markers resolved *E. lloense*, as here circumscribed, as two different clades not sister to each other (Vasco et al., in prep.). Because the plants in the two clades are indistinguishable morphologically, we prefer to treat them under the same name for now.

Additional specimens examined. BOLIVIA. **Cochabamba:** Prov. Carrasco, Siberia Este, Monte Hotel, *Fernández-Terrazas et al. 2537* (MO); Incachaca, *Steinbach 5870* (K, NY); Prov. Chapare, Incachaca-Chusi, *Steinbach 9211* (GH, MO, NY). **La Paz:** Prov. Nor Yungas, Est. Biol. Tunquini, senda paralela al camino principal a la mina hasta el pantano, *Bach 1881* (NY, UC); Chapare, along rd. toward Villa Tunari from Cochabamba, *Luer et al. 8682* (NY, SEL); Prov. Nor Yungas, 1.9 km NE of Chuspipata on the rd. to Coroico, *Solomon 14929* (MO, NY). **Santa Cruz:** Prov. Manuel María Caballero, camino a Siberia, 26 km de Comarapa, *Jordán & Vargas 338* (MO, NY, USZ); Prov. Manuel María Caballero, camino a Siberia, 26 km de Comarapa, *Jordán & Vargas 373* (MO, USZ).

COLOMBIA. **Antioquia:** Mpio. Jardín, vereda La Sesenia, sector La Orqueta, *Rodríguez et al. 4988* (HUA, NY); Mpio. Medellín, Correg. San Antonio de Prado, Alto del Silencio, vereda Potrerito, *Vasco 512* (HUA, MO, NY). **Boyacá:** margen del río Cusiana, finca Comijoque, *Hagemann 660* (COL); Cordilla Oriental, Vertiente W, carretera Sogamoso-Pajarito, valle del río Cusiana, *Jaramillo-M. et al. 3773* (COL). **Cauca:** Km. 62 on rd. from Tortoro to Inza, E of páramo de Guanacas, *Barrington 496* (COL). **Cundinamarca:** Patio Bonito, Batatas Valley, cordillera de Heliconia, 12 km SE of Gachalá, *Grant 10210* (COL, HUA). **Huila:** cordillera Oriental, Caquetá side of Huila–Caquetá divide, 20 km SE of Garzón, *Little 9377* (COL, F, GH). **Meta:** Mpio. Acacías, cordillera Oriental, Colonia Penal y Agrícola de Oriente, *Jaramillo-M. 7430* (COL); Mpio. San Juanito, PNN Chingaza, cañón del río Guajaro, *Vasco et al. 779* (HUA, NY). **Nariño:** carretera La Victoria (inspección de Policía Mpio. Ipiales)–Monopamba, Km. 32, Motilón, *Hagemann & Leist 1846* (COL); Mpio. Pasto, río San José, parte alta del río Bobo, *Ramírez & Cuayal 3848* (COL). **Putumayo:** above Sibundoy, *Alston 8375* (NY); páramo Quilinsayaco, *Hagemann & Leist 1997* (COL). **Risaralda:** Mpio. Pereira, orilla del camino entre Ceylan y el Cedral, *Franco et al. 2883* (COL); Mpio. Pueblo Rico, vereda Montebello, cerca de los Cajones, subiendo hacia la base militar, *Vasco et al. 646* (HUA, NY). **Valle del Cauca:** Mpio. El Cairo, cordillera Occidental, Serranía de los Paraguas, cerro del Inglés, *Silverstone-Sopkin et al. 2954* (NY).

COSTA RICA. **Puntarenas:** Cantón de Coto Brus, Zona Protectora Las Tablas, Cuenca Terraba-Sierpe, Sitio Coto Brus, *A. Rojas & E. Navarro 4350* (NY); same locality, *A. Rojas et al. 4923* (NY).

ECUADOR. **Azuay:** forested slopes betw. Sta. Cruz Pamba & Loma de Canela, in region of Río Sadracay, tributary of Río Mehuir, N of Melleturno, *Steyermark 52964* (F). **Bolivar:** bosque protector Cashca-Tooras, SE of Santiago, *Øllgaard & Navarrete 2077* (AAU); Simiatug, Had. Talahua, *Penland & Summers 651* (F). **Carchi:** valle de Maldonado, Km. 53 on rd. Tulcán–Maldonado, *Holm-Nielsen et al. 5657* (AAU, MO, UC); near encampment in Gualpi Chico area of Awá Reserve, *Hoover et al. 2897* (MO, QCA); rd. Tulcán–Maldonado, 49 km from Tulcán,

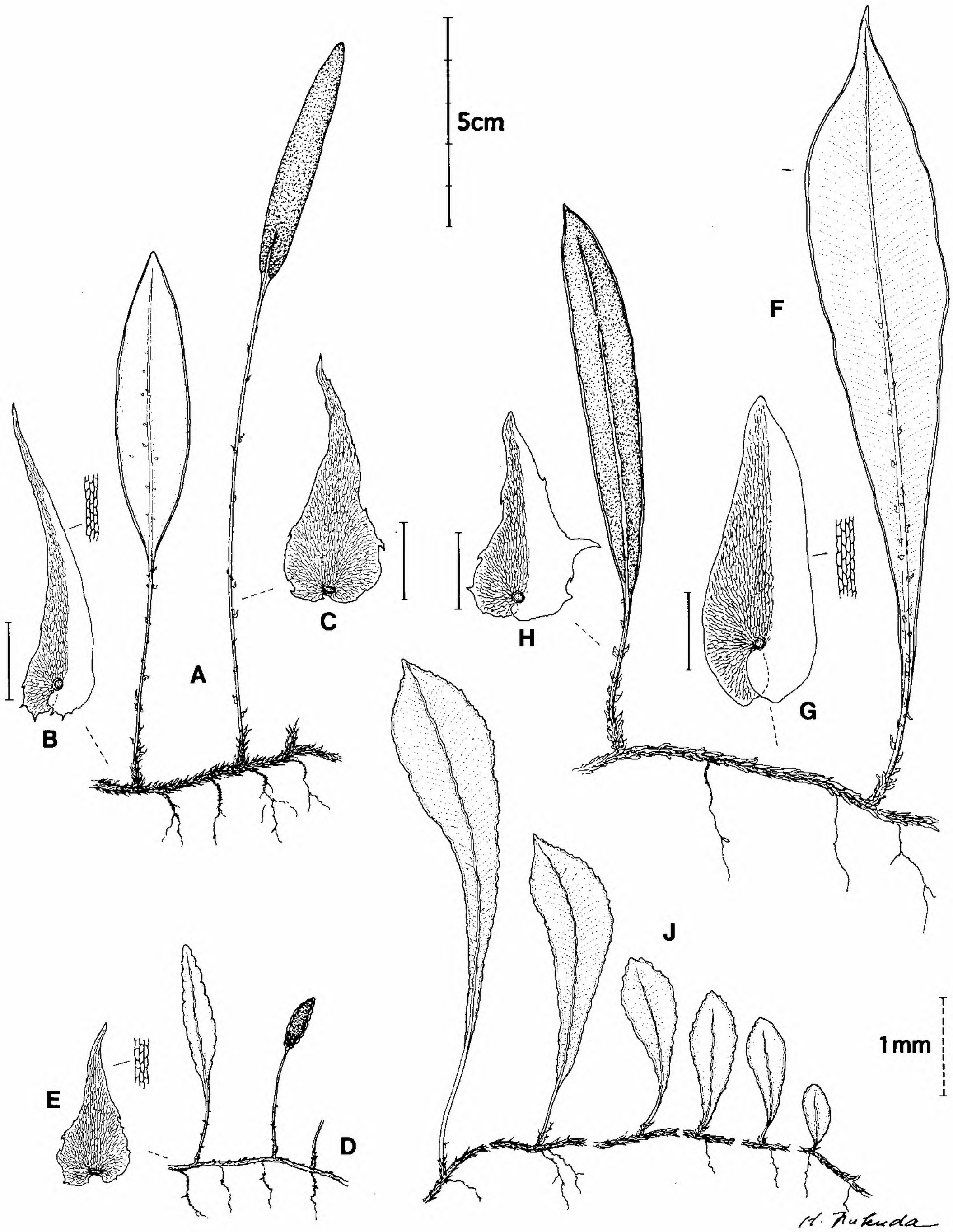


Figure 15. A–C. *Elaphoglossum minutum* (Pohl ex Fée) T. Moore. —A. Habit, with fertile leaf at right. —B. Rhizome scale. —C. Petiolar scale. D, E. *Elaphoglossum feei* (Bory ex Fée) T. Moore. —D. Habit, with fertile leaf at right. —E. Rhizome scale. F–J. *Elaphoglossum wrightii* (Mett. ex D. C. Eaton) T. Moore. —F. Habit, with one fertile leaf at left. —G. Rhizome scale. —H. Petiolar scale. —J. Heteroblastic leaf series. A–C from *Woodson Jr. et al. 1177* (NY); D, E from *Stehlé 2406* (NY); F–H from *Ekman 3882* (NY); J from *Shafer 4131* (NY). All habit illustrations conform to the 5-cm scale bar; all other scale bars equal 1 mm.

Øllgaard & Balslev 8334 (AAU, NY, QCA, UC). **Chimborazo:** rd. ca. 10 km NE of Alao, at Chuspipaccha, *Øllgaard et al. 38174* (AAU). **Imbabura:** Reserva Cotacachi–Cayapas, bosque protector Neblina, *Vasco et al. 865* (NY, QCA). **Loja:** Par. Nac. Podocarpus, above Nudo de Cajanuma, *Øllgaard et al. 74480* (AAU), *75008* (AAU, NY, QCA, QCNE); El Tiro, shrubby páramo along rd. Loja-Zamora, at highest point, ca. 10 km from Loja, *van der Werff et al. 19596* (MO, QCNE, UC). **Los Ríos:** summit of Cerro Samama (Hda. Clementina), S of rd. Caluma–Catarama, *Øllgaard & Navarrete 2049A* (AAU). **Morona-Santiago:** rd. Sta. Susana de Chiviasa-Panecillo, Km. 3–4, *Øllgaard & Navarrete 2658* (AAU, QCA), *2700* (AAU, QCA). **Napo:** camino Oyacachi–El Chaco, sector río Chalpi, ca. 15 km al E del pueblo, *Navarrete & Asimbaya 1644* (AAU, NY, QCA); Oyacachi, ca. 2 km below village, opposite abandoned village, Casajuchu, *Øllgaard & Navarrete 1222* (AAU, NY, QCA). **Pastaza:** rd. N of Mangayacu, Km. 1.8 W of Mera, disturbed forest along stream, *Øllgaard & Navarrete 105660* (AAU); rd. N of Mera, toward Río Anzu, Km. 6.7, *Øllgaard & Navarrete 105675* (NY, QCA). **Pichincha:** Salvador, ca. 25 km W of Quito, *Bell 665* (GH); Km. 17, Nono–Tandayapa, along Río Alambi, *Dodson & Clendenin 10815* (QCNE); Mt. Pululahua, *Mille 200* (COL); Mt. Pululahua, *Mille s.n.* (NY). **Tungurahua:** W of Río Guambi, ca. 7 km along rd. & trails S of Río Negro, *Øllgaard & Navarrete 3050* (AAU, QCA). **Zamora–Chinchipe:** Est. Científica San Francisco, study plot A9, along trail T1 above refuge, *Lehnert 1491* (NY, UC); Est. Científica San Franciso, ca. 35 km from Loja on rd. Loja–Zamora, quebrada de Milagro along T4, *Mendieta 162* (NY); Par. Nac. Podocarpus, rd. Yangana–Valladolid, just S of the pass (Nudo de Sabanilla), *Øllgaard 90658* (AAU).

PERU. **Cusco:** Urubamba, Machu Picchu, Llactapampa, a small pampa below palcay on the Aobamba river, *Peyton & Peyton 1100* (MO); Calca, rd. quebrada Alto Lacco, *van der Werff et al. 21197* (MO, UC). **Pasco:** Oxapampa, Distr. Huancabamba, sector Sta. Barbara–Milpo, *Mellado et al. 2767* (MO, USM); Oxapampa, Distr. Villa Rica, bosque de la reserva municipal El Sho'llet, Abra Villa Rica, *Mellado et al. 2981* (MO, UC, USM), *Mellado et al. 3026* (HUT, MO, NY, UC, USM).

VENEZUELA. **Aragua:** Colonia Tovar, *Fendler 286* (GH, K, MO, NY); Par. Nac. Henry Pittier, trail above Guamitas to summit of La Mesa, above El Limón, *Steyermark 89850* (GH, NY); Carretera Los Anaucos/Costa de Maya–Colonia Tovar, Monumento Nat. Pico Codazzi, *Vasco 845* (NY, VEN). **Táchira:** along quebrada Agua Azul, S of Reposo, 14 km SE of Delicias, *Steyermark & Liesner 118353* (MO, NY). **Trujillo:** Mpio. Boconó, Par. Nac. Guaramacal, páramo de Guaramacal, SW of the television antennas, *Stergios et al. 20664* (MO, NY), *20728* (MO, NY). **Vargas:** Monumento Nat. Pico Codazzi, *Mostacero et al. 325* (UC), *326* (UC), *355* (UC), *506* (UC).

10. Elaphoglossum minutum (Pohl ex Fée) T. Moore, Index Fil. 12: 361. 1857. Basionym: *Acrostichum minutum* Pohl ex Fée, Mem. Foug. [Hist. Acrost.] 2: 39, tab. 10, fig. 3. 1845. TYPE: Brazil. Goiás: "circa Goyaz," [15°55′S, 50°57′W], s.d., *J. B. E. Pohl 1432* (holotype, W!). Figures 6C, 10E–J, 15A–C.

Elaphoglossum revolutum (Liebm.) T. Moore, Index Fil. 365. 1862, syn. nov. Basionym: *Acrostichum revolutum* Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5, 1: 163. 1849. *Acrostichum revolutum* Liebm., Mexic. bregn. 163 (reprint 11). 1849, nom. illeg. TYPE: Mexico. Oaxaca: Chinantla, betw. Lobani & Petlapa, [17°28′N, 96°02′W], ca. 1000 m, s.d., *F. M. Liebmann s.n.* [Pl. Mex 2427, Fl. Mex. 4] (lectotype, designated by Mickel & Beitel [1988: 181], C!; isolectotypes, BM!, BM fragm. NY!, US!).

Elaphoglossum rampans (Baker) Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36: 56. 1899, syn. nov. Basionym: *Acrostichum rampans* Baker, Syn. fil. (ed. 2): 518. 1874. TYPE: Cuba. Oriente, 1865, *C. Wright 3959* (holotype, K!; isotypes, NY! [2], P!).

Elaphoglossum elegantulum Rosenst., Repert. Spec. Nov. Regni Veg. 10: 280. 1912, syn. nov. TYPE: Costa Rica. San José: San Cristobal, [9°47′N, 84°01′W], 1500 m, Aug. 1910, *C. Wercklé s.n.* (holotype, S!, S photos BM!, NY!).

Elaphoglossum macilentum Mickel, Fieldiana, Bot., n.s. 27: 144. 1991, syn. nov. TYPE: Peru. Madre de Dios: Prov. Manú, Par. Nac. Manú, Río Manú, Río Cumerjali, 71°32′W, 11°49′S, 350–450 m, 22 Oct. 1986, *R. B. Foster 11978* (holotype, F!, F photo NY!).

Elaphoglossum xiphoides Mickel, Ann. Missouri Bot. Gard. 78: 259–260, fig. 1C. 1991, syn. nov. TYPE: Venezuela. Bolívar: cuenca media del río Paragua, 06°03′N, 63°47′W, 13 June 1987, *B. Stergios 10310* (holotype, NY!; isotype, MO!).

Rhizomes ca. 1 mm wide, long-creeping; rhizome scales 1.5–3 mm, appressed, ovate-lanceolate, entire, light orange to brown, concolorous, dull. Sterile leaves 4.5–19.5 cm; petioles 0.3 to 0.8 times the lamina length; petiolar scales 1–2 mm, clasping to slightly spreading, ovate, entire or with small marginal projections, light orange to brown, dull; laminae 2.5–13.5 × 0.5–2.1 cm, 3.8 to 11 times longer than wide, coriaceous, simple, narrowly elliptic to oblong, usually widest at or above the middle and parallel-sided medially, margins entire, apices obtuse, bases cuneate; adaxial lamina surface scales absent; abaxial lamina surface scales absent or sparse and only near the costa, the scales 1–3 mm, ovate, brown, dull. Fertile leaves 6–18 cm; petioles (0.8 to)1.8 to 3.3 times the lamina length; laminae 2–9.5 × 0.4–1 cm, oblong, entire; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum minutum* occurs in Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Peru, and Venezuela, at elevations of 100–1000(1700) m.

Discussion. *Elaphoglossum minutum* has the lowest elevational range of any species of *Elaphoglossum* sect. *Squamipedia*, being found typically from 100 to 1000 m in elevation. It resembles *E.*

squamipes and *E. lloense* in lamina shape (Fig. 10) and, like them, is widespread in tropical America. It differs from both species by the relatively shorter petioles of the sterile leaves and laminae that tend to be more oblong and parallel-sided in the middle. From *E. squamipes* it further differs by its generally narrowly elliptic laminae (instead of the ovate-lanceolate laminae of *E. squamipes*).

The name *Elaphoglossum minutum* has often been misapplied (e.g., by Mickel, 1991, 1995a, 1995b) to *E. gayanum* (Fée) T. Moore, a species belonging to *Elaphoglossum* sect. *Lepidoglossa* Christ. *Elaphoglossum minutum* and *E. gayanum* are superficially similar in their laminae, which are slightly coriaceous and typically oblong and parallel sided in the middle. *Elaphoglossum gayanum*, however, differs by terrestrial habit, presence of phyllopodia, short-creeping rhizomes, and rhizome scales with sclerotic stripes (vs. epiphytic habit, no phyllopodia, long-creeping rhizomes, and concolorous rhizome scales in *E. minutum*). In herbaria, specimens of *E. gayanum* are often also identified as *E. leptophyllum* (Fée) T. Moore, a synonym of *E. gayanum*.

Additional specimens examined. BOLIVIA. **Beni:** Prov. Ballivián, 16 km por el camino maderero, 12 km de Yucumo a Rurrenabaque, *Kessler et al. 10944* (UC). **Cochabamba:** Prov. José Carrasco Torrico, Par. Nac. Carrasco, al S del Campamento Petrolero Ichoa, *Aceby 490* (NY); Prov. Chapare, Par. Nac. Carrasco, cavernas del Repechón, *Kessler et al. 8300* (NY, UC). **La Paz:** Prov. Sud Yungas, *Krömer & Acebey 298* (UC).

BRAZIL. **Goiás:** Goiania, *Brade 15379* (MO, NY, RB).

COLOMBIA. **Magdalena:** Sta. Marta, *Smith 2673* (F, GH, K, NY).

COSTA RICA. **Cartago:** Turrialba, near Interamerican Inst., *Scamman 5996* (GH). **Guanacaste:** Cantón de La Cruz, P. N. Guanacaste Volcán Orosí La Cruz, Martza, *Rojas et al. 3096* (MO, NY). **Puntarenas:** Cantón de Coto Brus, cuenca Terraba-Sierpe, Sabalito, Mellizas, finca Cafrosa, sendero ripario orillas río Quijada del Diablo, *Rojas et al. 4354* (MO, NY); Cantón de Coto Brus, cuenca Térraba-Sierpe, finca Cafrosa, orillas del río Negro, *Rojas et al. 4892* (MO).

CUBA. **Santiago de Cuba:** pico Turquino, arroyo Bayajá, Nagua region, *Ekman 14764* (NY); N spur of Sierra Maestra, W of Río Yao, *Morton & Acuña 3382* (GH, NY, UC); prope Monte Verde, *Wright 968* (GH). **Villa Clara:** Trinidad Mtns., near La Vega, E of Loma Ventana, *Webster et al. 240* (GH). **Unknown:** Oriente, arroyo Veintecineo, Los Organos, *Wright 1071* (GH, MO).

DOMINICAN REPUBLIC. **Santiago:** Distr. San José de las Matas. Jicomé, Loma del Medio, Jicomé, *Valeur 640* (F, GH, MO, NY). **Santiago Rodríguez:** N side of cordillera Central, arroyo Caña, 27 km SW of Cepillo part of Monción, 1 km past pueblo of Aguacate, *Mickel et al. 8601* (MO, UC).

ECUADOR. **Napo:** Añangu, S bank of Río Napo 95 km downstream from Coca, *Balslev et al. 60594* (AAU); Tiputini Biodiversity Station, *Köster et al. 871* (NY); outside of Par. Nac. Yasuni, ca. Km. 21 on Maxus Oil Company rd., transect 11, *Moran et al. 6206* (NY).

GUATEMALA. **Alta Verapaz:** Cerro Chinajá, betw. finca Yalpemech & Chinajá, above source of Río San Diego, *Steyermark 45613* (F); Cubilguitz, *von Tűrckheim 159* (GH). **Huehuetenango:** Cerro Victoria, across river from finca San Rafael, Sierra de los Cuchumatanes, *Steyermark 49613* (F, GH).

GUYANA. Region U. Takutu-U. Essequibo, Kassikaityu river, 0–5 km E of camp, *Clarke 4963* (NY).

HONDURAS. **Comayagua:** above El Achote, hills above the plains of Siguatepeque, *Yuncker et al. 6440* (GH, NY).

JAMAICA. **St. Elizabeth:** Gorge of Jones river, N of Ginger hill, *Proctor 22170* (GH, NY).

MEXICO. **Chiapas:** Mpio. Ocozocoautla de Espinosa, Selva de Ocote, 32 km NW of Ocozocoautla, *Breedlove 27432* (NY); Ocozocoautla de Espinosa, Selva del Ocote, 32 km NW of Ocozocoautla, *Breedlove 27432* (F, MO); Palenque, along Hwy. 199 from Palenque to Ocosingo, 43 mi. SW of Palenque, *Croat 40328* (MO, UC); Ocosingo, en laguna Ocotalito, a 12 km al NE de Monte Líbano camino a Chancala, *Martínez-Salas & Soto 18661* (F); Ocosingo, a 3 km al S de Naja, camino a Palenque, *Martínez-Salas & Stevens 23981* (MO, NY). **Oaxaca:** Distr. Cuicatlán, vic. of Teutila, *Mickel 7326* (NY). **Veracruz:** region of San Andrés Tuxtla, near Zapoapan, SE of Catemaco, *Dressler & Jones 86* (GH); Mpio. Mecayapan, faldas del Volcán Sta. Marta, Ejido Plan Agrario, *Krömer & Otto 2873* (NY, UC).

PANAMA. **Chiriquí:** Boquete, *Davidson 746* (GH, MO); vic. of Boquete, *Woodson Jr. & Schery 765* (GH, MO); Distr. Boquete, finca Lérida to Boquete, *Woodson Jr. et al. 1177* (MO, NY).

11. Elaphoglossum moorei (E. Britton) Christ, Bull. Herb. Boissier, sér. 2, 3: 148. 1903. Basionym: *Acrostichum moorei* E. Britton, Mem. Torrey Bot. Club 4: 273. 1895. *Rhipidopteris rusbyi* Christ, Farnkr. Erde 46. 1897, nom. superfl., based on the same type gathering as *A. moorei*. *Elaphoglossum bangii* Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36(1): 99, fig. 51. 1899, nom. superfl. *Microstaphyla bangii* (Christ) Hieron., Bot. Jahrb. Syst. 34: 539. 1904, comb. superfl. *Microstaphyla moorei* (E. Britton) Underw., Torreya 5: 88. 1905. *Peltapteris moorei* (E. Britton) L. D. Gómez, Brenesia 6: 30. 1975. TYPE: Bolivia. La Paz: Yungas, 1890, *M. Bang 558* (lectotype, designated by Mickel in Tryon & Stolze [1991], NY! [3]; isotypes, BM!, MO!, UC not seen, US!). Figures 6A, 7F–J, 8L.

Elaphoglossum peruvianum (L. D. Gómez) Mickel, Brittonia 32: 116. 1980. Basionym: *Peltapteris peruviana* L. D. Gómez, Rev. Biol. Trop. 18(1–2): 217, fig. 1. 1971. TYPE: Peru. Cuzco: alturas de Sicre, 3030 m, June 1924, *C. Bües 1572* (holotype, US!).

Rhizomes 0.6–0.9 mm wide, long-creeping; rhizome scales 1–2 mm, appressed, lanceolate, subentire, with occasional projections, light orange to brown, dull. Sterile leaves 3–17 cm; petioles about equaling the lamina length; petiolar scales 0.8–1.5

mm, scattered, clasping to spreading, ovate, with small marginal projections, brown; laminae 2–9 × 1.5–3 cm, 1.5 to 3.5 times longer than wide, chartaceous, pinnately divided, lanceolate to oblong, margins entire, apical segment similar to lateral ones, bases truncate, pinnae 0.4–1 mm wide, 8 to 17 pairs, spreading to ascending, sometimes notched or divided at the apex; adaxial lamina surface glabrous to sparsely scaly, the scales 0.1–0.5 mm, brown, sometimes darker at the point of attachment; abaxial lamina surface sparsely scaly, the scales 0.1–1 mm, with small marginal projections, brown, sometimes darker at point of attachment. Fertile leaves 6.5–13 cm; petioles 4 to 6 times the lamina length; laminae 1.6–3 × 0.4–0.5 cm, oblong, subentire to serrate or shallowly lobed, apices rounded, base truncate; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum moorei* occurs in Bolivia and Peru, where it is epiphytic in cloud forests at elevations of 1400–2400 m.

Discussion. *Elaphoglossum moorei* and *E. colombianum* are the only Neotropical species of *Elaphoglossum* with laminae that are pinnately divided (Fig. 7). The number and width of the segments can distinguish them, with eight to 17 in *E. moorei*, but fewer (five to nine) in *E. colombianum*. Pinna bases are narrower in *E. moorei*, only to 1 mm widths, but range from 1 to 2 mm in *E. colombianum*. The two species are distinct geographically (Peru and Bolivia, *E. moorei*; restricted to Colombia, *E. colombianum*). Some specimens of *E. moorei* (cited below) bear laminae that are broadly cut and serrate to variously lobed (Fig. 8K). The variation in dissection suggests hybridity, but one of the specimens (*Vásquez et al. 30126*) has fertile leaves with well-formed spores, suggesting that these plants may not be hybrids. The exact nature of these plants still needs to be determined, but are accepted within *E. moorei*, pending further investigation.

Additional specimens examined. BOLIVIA. **Cochabamba:** Prov. Carrasco, exposición SW, *Fernández-Terrazas et al. 2419* (BOLV, MO); Prov. Chapare, *Steinbach 9301* (GH, MO, NY, UC). **La Paz:** Prov. Franz Tamayo, Par. Nac. Madidi, Mojos, campamento Fuertecillo, sobre la senda a Queara, *Cayola et al. 2847* (LPB, MO, NY, USZ); Prov. Franz Tamayo, Par. Nac. Madidi, Mojos, campamento inciensal Linter, 2 km al NW del campamento Fuertecillo (camino de herradura hacia Queara), *Fuentes et al. 11706* (LPB, MO).

PERU. **Cusco:** La Convención, Distr. Sta. Ana, Madre Selva, *Valenzuela et al. 3082* (CUZ, MO, UC); La Convención, Distr. Sta. Ana, Tunkimayo, *van der Werff et al. 21477* (MO, NY, UC). **Pasco:** Oxapampa, Distr. Villa Rica, bosque de la reserva municipal El Sho'llet, Abra Villa Rica, *Mellado et al. 3018* (AMAZ, HUT, MO, NY, UC, USM); Oxapampa, Distr. Huancabamba, P. N. Yanachaga-Chemillén, sector Quebrada Yanachaga, *Vásquez et al. 30581* (AMAZ, HUT, MO, MOL, NY, UC, USM); Oxapampa, Distr. Huancabamba, Par. Nac. Yanachaga-Chemillén, sector San Daniel, *Vásquez et al. 31008* (AMAZ, HUT, MO, NY, UC, USM).

Specimens of Elaphoglossum moorei with irregularly cut laminae. BOLIVIA. **Cochabamba:** Prov. Carrasco, Km. 117 on old rd. Cochabamba-Villa Tunari, *Kessler et al. 7078* (NY). **La Paz:** Prov. Nor Yungas, Chuspipata, sendero a la mina San Juan, *Lehnert 384* (NY).

PERU. **Cusco:** La Convención, Distr. Huayapata, San Cristóbal, *van der Werff et al. 21437* (MO, NY). **Pasco:** Oxapampa, Distr. Huancabamba, sector Milpo, *Vásquez et al. 30126* (MO, USM).

12. Elaphoglossum nidiforme Mickel, Fieldiana, Bot., n.s. 27: 148. 1991, as "*nidiformis*." TYPE: Peru. Madre de Dios: Manú, Cerro de Pantiacolla, Río Palotoa, 10–15 km NNW of Shintuya, [12°34′S, 71°15′W], 15 Dec. 1985, *R. B. Foster 10891* (holotype, F!; isotype, USM). Figures 9B, 11A–D.

Rhizomes ca. 10 mm wide, short-creeping to compact; rhizome scales 4–6 mm, spreading, ovate to lanceolate, entire or nearly so, orange to light brown, lustrous. Sterile leaves 30–37 cm; petioles 0.02 to 0.1 times the lamina length; petiolar scales 2–5 mm, speading, ovate, entire, light orange to brown, concolorous; laminae 28–35 × 4–5 cm, 4 to 6 times longer than wide, coriaceous, simple, narrowly oblanceolate, margins entire, apices acute, bases narrowly and gradually decurrent; adaxial lamina surface scales absent; abaxial lamina surface scales absent or, if present, the scales 0.2–0.3 mm, scattered, appressed, stellate. Fertile leaves 30–40 cm; petioles ca. 0.5 times the lamina length; laminae 20–32 × 3–4 cm, narrowly oblanceolate, entire, the apices acute, bases narrowly decurrent; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum nidiforme* occurs in Bolivia, Ecuador, and Peru, at elevations of 700–2000 m.

Discussion. *Elaphoglossum nidiforme* is highly atypical morphologically within *Elaphoglossum* sect. *Squamipedia* and is included here on the basis of chloroplast DNA sequence data (Rouhan et al. 2007; Vasco et al., in prep.). It is atypical in its nest-forming habit, compact rhizomes, absence of peglike aerophores, presence of phyllopodia, extremely short petioles, sterile leaves 30–37 cm long, and oblanceolate laminae. By these characters it more closely resembles a member of *Elaphoglossum* sect. *Elaphoglossum*; however, the thin, light orange to brown

scales on the petiole bases and proximal portions of the rachises suggest *Elaphoglossum* sect. *Squamipedia*, as do the echinulate spores (Moran et al., 2007). Curiously, a Madagascan species, *E. nidusoides*, resembles *E. nidiforme* (its specific epithet refers to the resemblance). As indicated by molecular sequence data, *E. nidusoides* belongs to *Elaphoglossum* sect. *Squamipedia* and is sister in analyses to another Madagscan endemic, *E. marojejyense* (Rouhan et al., 2007). The latter species morphologically resembles the typical Neotropical members of *Elaphoglossum* sect. *Squamipedia*, except for its perispore morphology, which is non-echinulate (Moran et al., 2007). Thus, it appears that there have been two independent origins in the evolution of large, non-creeping and nest-forming species within *Elaphoglossum* sect. *Squamipedia* in the Andes and Madagascar. Besides the two Madagascan taxa mentioned above, there are no other taxa of *Elaphoglossum* sect. *Squamipedia* outside of the Neotropics.

Additional specimens examined. BOLIVIA. **Cochabamba:** Prov. José Carrasco Torrico, 141 km antigua carretera Cochabamba-Villa Tunari, *Kessler et al. 7689* (NY), *Kessler et al. 7948* (NY, UC). **La Paz:** Prov. Caranavi, serranía de Bella Vista, pasando la cumbre en dirección a Caranavi, *Jiménez 2191* (NY); Prov. Caranavi, Comunidad Cultural Unidos, 36 km de Caranavi hacia Sapecho, *Kessler et al. 11690* (NY). **Unknown:** *Jiménez 2274* (LPB, NY, UC).

ECUADOR. **Zamora-Chinchipe:** Reserva San Francisco, ca. 30 km from Loja on new rd. Loja–Zamora, *Lehnert & Kessler 1316* (NY, UC); area of Est. Cienfífica San Francisco, ca. 30 km on rd. Loja–Zamora E of Ceja andina, *Werner 466* (NY).

13. Elaphoglossum peltatum (Sw.) Urb., Symb. Antill. 4: 61. 1903. Basionym: *Osmunda peltata* Sw., Prodr. 127. 1788. *Acrostichum peltatum* (Sw.) Sw., J. Bot. (Schrad.) 1800 (2): 11. 1801. *Rhipidopteris peltata* (Sw.) Schott ex Fée, Mém. Foug. [Hist. Acrost.] 2: 14. 1845. *Peltapteris peltata* (Sw.) C. V. Morton, Amer. Fern J. 45: 13. 1955. TYPE: Jamaica. s.d., *O. Swartz s.n.* (holotype, S!; isotypes, B!, B photo COL!).

Rhizomes ca. 1 mm wide, long-creeping; rhizome scales 1–2.5 mm, spreading to appressed, lanceolate, entire or nearly so, light orange to brown, dull. Sterile leaves 1.8–15 cm; petioles 0.5 to 0.8 times the lamina length; petiolar scales 1–2 mm, ovate to narrowly lancolate, concolorous; laminae 0.8–6 × 0.9–6 cm, ca. as long as wide, simple to 7 times dichotomously divided, circular to flabellate or lunate, apices obtuse, bases cordate to flabellate, segments 0.5–1.5 mm wide, linear; adaxial lamina surface scales absent; abaxial lamina surface scales absent or, if present, the scales 0.3–1.5 mm, ovate, nearly entire. Fertile leaves 2.6–8 cm; petioles 3 to 8 times the lamina length; laminae 0.5–20 × 0.5–20 mm, circular, margins entire or slightly crenate, apices rounded, bases cordate; intersporangial scales absent.

Distribution and elevation. *Elaphoglossum peltatum* is distributed in Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, Guadeloupe, Guatemala, Guyana, Haiti, Honduras, Jamaica, Martinique, Mexico, Nicaragua, Panama, Peru, Puerto Rico, and Venezuela. It is epiphytic on mossy trunks and fallen logs and occurs in wet montane forests typically at middle and upper elevations. *Elaphoglossum peltatum* has been collected from across its range from (0 to)500 to 3000 m.

Discussion. Several forms of *Elaphoglossum peltatum* have been recognized, based on dissection of the sterile laminae (Fig. 13). These range from undivided leaf laminae (forma *standleyi*), to once or twice divided (forma *flabellatum* (Humb. & Bonpl. ex Willd.) Mickel), to three to seven times divided (forma *peltatum*). The forms appear quite distinct from each other and may even grow intermixed, maintaining their distinctness, as often occurs with forma *peltatum* and forma *standleyi* (Moran, pers. obs.). Examination of herbarium specimens, however, reveals many intermediates among all the forms. Unpublished molecular phylogenetic results (Vasco et al., in prep.) suggest that although all three forms are a clade, each form may have had multiple origins within the clade. For these two reasons, and the fact that historically "forms" have been used, we decided to recognize the differences at the taxonomic level as forms and not as varieties.

13a. Elaphoglossum peltatum (Sw.) Urb. f. **flabellatum** (Humb. & Bonpl. ex Willd.) Mickel, Brittonia 32: 116. 1980. Basionym: *Acrostichum flabellatum* Humb. & Bonpl. ex Willd., Sp. Pl. 5: 110. 1810. *Elaphoglossum flabellatum* (Humb. & Bonpl. ex Willd.) Christ, Neue Denkschr. Allg. Schweiz. Ges. Gesammten Naturwiss. [Monogr. *Elaph.*] 36: 58, fig. 21. 1899. *Peltapteris flabellata* (Humb. & Bonpl. ex Willd.) C. V. Morton, Amer. Fern J. 45: 13. 1955. *Peltapteris peltata* f. *flabellata* (Humb. & Bonpl. ex Willd.) L. D. Gómez, Brenesia 6: 28. 1975. *Rhipidopteris flabellata* (Humb. & Bonpl. ex Willd.) Fée, Mém. Foug. [Hist. Acrost.] 2: 78. 1845. TYPE: [Probably Venezuela or Colombia.] "America meridionali," *A. von Humboldt & A. Bonpland s.n.* (holotype, B-W-19530!). Figures 8G, H, 9C, 13D–K.

Acrostichum flabellatum var. *sphenophyllum* Kunze, Linnaea 9: 32. 1834. *Acrostichum sphenophyllum* (Kunze) Kunze, Analecta Pteridogr. 11, tab. 7. 1837. *Rhipidopteris sphenophylla* (Kunze) Fée, Mém. Foug. 2: 79. 1845. TYPE: Peru. Loreto: ad arbores sylvar. fl. Peruv. prope Pampayaco, 1829, *E. Poeppig s.n.* (lectotype, designated here, PR!; isolectotypes, B not seen, PR fragm. NY!).

Acrostichum flabellatum var. *bipartitum* Sodiro, Crypt. Vasc. Quit. 489. 1893. TYPE: Ecuador. Pichincha: crece en la región tropical, la variedad "beta" en la región cerca de la confluencia del río Napo con el Pilatón, s.d., *A. Sodiro s.n.* (holotype, P not seen).

Acrostichum peltatum var. *potentillifolium* Christ, Bull. Soc. Bot. Belgique 35(1): 242. 1896. *Peltapteris peltata* f. *potentillifolia* (Christ) C. F. Reed, Amer. Fern J. 51: 98. 1961. *Elaphoglossum peltatum* f. *potentillifolium* (Christ) Mickel, Brittonia 32: 116. 1980. TYPE: Costa Rica. San José: La Palma, [10°03′N, 83°59′W], 18 Dec. 1988, *H. Pittier 704* (holotype, P!; isotype, CR!).

Rhizomes 1–2 mm wide, long-creeping; rhizome scales 1–2.5 mm, spreading to appressed, lanceolate, entire or nearly so, light orange to brown, dull. Sterile leaves 1.8–6 cm; petioles 1 to 3 times the lamina length; petiolar scales 1–2 mm, clasping to slightly spreading, ovate to narrowly lancolate, with marginal teeth or processes toward the base, brown, dark at point of attachment; laminae 0.8–1.5 × 1–3.6 cm, 1 to 1.5 times as long as wide, chartaceous, dichotomously divided 1 to 2 times, flabellate, minutely crenulate on distal margins, apices broadly obtuse, rarely notched, bases cuneate, segments (1–)4–9 mm wide, cuneate, crenulate distally with entire sides; adaxial lamina surface scaly, the scales either ca. 0.3 mm and circular or 0.5–1 mm, ovate, with marginal processes, sometimes hastate, light brown to dark brown; abaxial lamina surface with scales like those adaxially. Fertile leaves 2.6–8 cm; petioles 3 to 8 times times the lamina length; laminae 0.5–1.2 × 0.6–1.1 cm, circular, margins entire or slightly crenate, apices rounded, bases cordate; intersporangial scales inconspicuous to conspicuous, 1–1.5 mm, brown, lanceolate, with marginal processes.

Distribution and elevation. *Elaphoglossum peltatum* f. *flabellatum* occurs in Bolivia, Colombia, Costa Rica, Ecuador, Guyana, Panama, Peru, and Venezuela. The form occurs in wet forests, at elevations of 400–2400 m.

Discussion. *Elaphoglossum peltatum* f. *flabellatum* is distinguished by sterile laminae isodichotomously divided one or two times. The blade segments are often 4–9 mm wide, cuneate, and crenulate distally, with entire margins. The holotype of *Acrostichum flabellatum* var. *sphenophyllum* Kunze at LZ was destroyed during World War II, thus the designation above of a lectotype at PR.

Additional specimens examined. BOLIVIA. **La Paz:** Prov. Nor Yungas, Est. Biol. Tunquini, *Eberhardt et al. 598* (NY, UC).

COLOMBIA. **Antioquia:** W from Panamer. Hwy. 5 km down rd. to San Fermín de Briceño, ca. 25 km N of Yarumal, *Luteyn et al. 10765* (COL, NY, UC); Mpio. de Briceño, correg. de San Fermín, finca de los Montoya, 2 km de la vía que de Ventanas conduce a Briceño, *Vasco et al. 452* (HUA, NY). **Caldas:** Río Sta. Rita, Salento, *Killip & Hazen 9012* (GH, NY). **Cauca:** W flank of cordillera Occidental, W of Tambo, *Haught 5234* (COL, NY); Popayán, *Lehmann 1041* (GH, NY); Panamer. Hwy. betw. Calibío & Piendamó, *Plowman & Vaughan 5378* (COL, GH). **Chocó:** Mpio. San José del Palmar, vereda La Holanda, *Franco et al. 1259* (COL, MO). **Cundinamarca:** San Antonio Valley, 15 km SE of Gutiérrez, 60 km S of Bogotá, *Grant 9815* (COL, NY). **Magdalena:** Sierra Nevada de Sta. Marta, quebrada Indiana, *Kirkbride Jr. 1925* (COL, NY, UC); Sierra Nevada de Sta. Marta, finca Reflejo, quebrada La Sirena, *Kirkbride Jr. 2127* (COL, NY, UC). **Nariño:** Mpio. Tumaco, Km. 90, a 20 km de La Guayacana, *Mora 4257* (COL); Mpio. Ricaurte, *von Sneidern 624* (GH, MO). **Risaralda:** Mpio. Mistrató, arriba del río Currumay vía Puerto de Oro, *Orozco et al. 2165* (COL). **Santander:** Mpio. Charala, Correg. Virolín, Cañaverales near finca Sta. Helena, *Sipman & Aguirre 27574* (COL). **Valle del Cauca:** Mpio. de Argelia, vereda La Bella, finca La Miranda, *Franco et al. 1869* (COL); La Cumbre, cordillera occidental, *Killip 11619* (GH, NY).

COSTA RICA. **Alajuela:** 8 km N of San Ramón & 4 km W on side rd., *Mickel 3623* (NY); Cantón de San Ramón, Reserva Forestal San Ramón, cordillera de Tilarán, sendero el Polígono, *Rojas 2618* (MO, NY). **Cartago:** Sta. Clara de Cartago, *Maxon & Harvey 8251* (GH, NY, UC); Cantón de Paraíso, Par. Nac. Tapantí, cuenca del Reventazón, sendero Árboles Caídos y Oro Péndula, *Rojas et al. 4851* (MO, NY); ca. 12 km S of Cartago, *Tryon & Tryon 7060* (GH). **Guanacaste:** Cantón de Abangares, Upper San Gerardo Valley, 5 km N Monteverde, Atlantic slope/continental divide, *Haber & Zuchowski 9563* (MO); Par. Nac. Guanacaste Est. Pitilla, fila Orosilito, *Hammel et al. 17461* (MO). **Heredia:** Braulio Carillo Nat. Park, *Hennippam et al. 6878* (MO). **Limón:** Cantón de Limón, R. I. Chirripó, fila de Matama, a orillas de una de las quebradas del Río Bolley, *Rojas et al. 2323* (MO); Cantón de Limón, R. I. Chirripó, fila de Matama, río Bolley, filas paralelas a los ramales del río, *Rojas et al. 2380* (MO). **Puntarenas:** Cantón de Puntarenas, Reserva Biol. Monteverde, 2 km NE Sta. Elena, *Haber 8536* (MO); Monte Verde, ca. 40 km N of Interamer. Hwy., *Mickel 3604* (NY). **San José:** Cantón de Perez Zeledón, cordillera de Talamanca, Las Nubes de Sta. Elena, sendero El Gringo, *Alfaro 523* (NY); Cantón de Moravia, La Hondura (bajo la Hondura) rd. to Río Claro, *Wagner & Wagner 77055* (MO, NY, UC).

ECUADOR. **Carchi:** Río Blanco drainage above Chical, tributary of Río San Juan, ca. 12 km W of Maldonado, *Gentry & Shupp 26546* (MO, QCA); trail from Rafael Quindí's finca back toward Untal to stream, ca. 0.5 km from finca, *Hoover & Wormley 1611* (MO). **Imbabura:** Ibarra, Lita, comunidad San Francisco, next to Río Verde, 13 air km S of Lita, *Clark et al. 7513* (NY); vic. of Río Verde, ca. 5 km SW from village of Maní, Río Cachaco, *Sperling & Bleiweiss 5018* (GH, QCNE). **Napo:** Archidona, carr.

Hollin–Loreto, Km. 25, sector Challua Yacu, *Cerón & Hurtado 6465* (MO, QCNE, UC); rd. Baeza–Tena, 6.8 km from Baeza, *Øllgaard 99984* (AAU, QCA, QCNE). **Pichincha:** rd. Pacto–La Delicia–La Esperanza, Km. 19.5, *Øllgaard et al. 2241* (AAU, QCA); Km. 36 along rd. to SE from La Aurora (Km. 7 on Sto. Domingo–Quevedo rd.), passing through La Reforma, *Øllgaard 98068* (AAU). **Zamora-Chinchipe:** S & SE of Zamora, *Øllgaard et al. 74861* (AAU, QCA); area of Est. Cientifica San Francisco, rd. Loja–Zamora, ca. 35 km from Loja, *Werner 688* (MO, NY, QCNE).

GUYANA. Upper Mazaruni river region, Karowtipu Mt., *Boom & Gopaul 7460* (NY); Upper Potaro river region, upper slopes of Mt. Wokomung, *Boom & Samuels 9195* (NY).

PANAMA. **Bocas del Toro:** Cerro Colorado, ca. 12 mi. from Camp Chami [Chame], *McPherson 9529* (MO). **Chiriquí:** Fortuna Dam area, along Quebrada Bonito to E of rd., *Churchill et al. 4839* (MO). **Panamá:** Par. Nac. Altos de Campana, sendero de interpretación, *Correa et al. 8586* (NY); area surrounding Rancho Chorrots above Torti Arriba, Canazas Mtn. chain, *Folsom et al. 6677* (AAU, NY).

PERU. **Amazonas:** *Woytkowski 8297* (GH, MO). **Ayacucho:** Aina, betw. Huanta & Río Apurimac, *Killip & Smith 22781* (NY); Carrapa, betw. Huanta & Río Apurimac, *Killip & Smith 23206* (GH, NY). **Cajamarca:** San Ignacio, Distr. Huarango, Poblado Selva Andina, trocha de captación de agua, *Perea & Mateo 2951* (AMAZ, HUT, MO, MOL, NY, USM). **Cusco:** Paucartambo, *Vargas-Calderón 6786* (MO). **Junín:** near La Merced, Villa Amoretti, *Kunkel 632* (GH); Satipo, rd. from Satipo to Comamanta, Ponte Pomay, *Weigend et al. 5755* (MO, NY). **Madre de Dios:** Manú, Cerro de Pantiacolla, Río Palotoa, 10–15 km NNW of Shintuya, *Foster et al. 10894* (AAU, GH, NY, UC). **Pasco:** Oxapampa, Abra los Melliza, 4–8 km from Eneñas, *Skog et al. 5039* (NY); Oxapampa, Gran Pajonal, near Chequitavo, *Smith 5310* (AAU, MO, NY). **San Martín:** Rioja, Venceremos, Km. 391 Bagua-Moyobamba rd., *Smith et al. 5960* (MO); near Tarapoto, *Spruce 4635* (NY).

VENEZUELA. **Amazonas:** Mpio. Atures, 8 km NW of settlement of Yutaje, plateau 3 km W of Río Coro-Coro, W of Serranía de Yutaje, valley E base of unnamed 1760 m peak, *Liesner & Holst 21548* (MO, NY, UC). **Barinas:** Distr. Bolívar, entre Santo Domingo y Altamira, Quebradón, en el camino que lleva al tunel que va hacia la represa, *Ortega & van der Werff 2356* (MO, NY, UC). **Mérida:** Río Albariga, N of Mérida, *Alston 6982* (MO), *Moritz 313* (NY). **Portuguesa:** Selva nublada, 15 km al E de Chabasquón, 67 km al NNO de Guanare, *Steyermark et al. 126785* (MO, UC). **Zulia:** Perijá, Sierra de Perijá, loma arriba de la quebrada del río Omira-kumá (Tumuriasa), cerca de la frontera Colombo-Venezolana SW de Pishikakao e Iría hacia la Misión de Sucurpo, *Steyermark & Dunsterville 105673* (NY).

13b. **Elaphoglossum peltatum** (Sw.) Urb. f. **peltatum**. Figures 8A–E, J, 9A, 13L–S.

Elaphoglossum peltatum f. *foeniculaceum* (Hook. & Grev.) Mickel, Brittonia 32: 116. 1980. Basionym: *Acrostichum foeniculaceum* Hook. & Grev., Icon. Filic. tab. 119. 1829. *Elaphoglossum foeniculaceum* (Hook. & Grev.) C. Chr., Index Filic. 307. 1906 [1905]. *Peltapteris peltata* f. *foeniculacea* (Hook. & Grev.) C. V. Morton, Amer. Fern J. 45: 13. 1955. *Peltapteris foeniculacea* (Hook. & Grev.) L. D. Gómez, Brenesia 6: 28. 1975. TYPE: Ecuador. Esmeraldas: Esmeralda, s.d., 3000 m, *W. Jameson s.n.* (holotype, K!).

Rhizomes 1–2 mm wide, long-creeping; rhizome scales 2–3.5 mm, spreading to appressed, lanceolate, entire or nearly so, light orange to brown, dull. Sterile leaves 3.5–10 cm; petioles 1.2 to 3 times the lamina length; petiolar scales 2–3 mm, clasping to slightly spreading, ovate to narrowly lancolate, with marginal teeth or processes toward the base, brown, concolorous; laminae 2–2.7 × 2.3–6 cm, 1 to 1.6 times as long as wide, chartaceous, dichotomously divided 3 to 7 times, flabellate, minutely crenulate on distal margins, apices broadly obtuse, rarely notched, bases cuneate, segments 1–2 mm wide; adaxial lamina surface scaly, the scales either ca. 0.3 mm and circular or 1–1.5 mm, ovate, with marginal processes, sometimes hastate, light brown to dark brown; abaxial lamina surface with scales like those adaxially. Fertile leaves 3–3.4 cm; petioles 3 to 8 times the lamina length; laminae 0.8–1.2 × 0.8–1.5 cm, circular, margins entire or slightly crenate, apices rounded, bases cordate; intersporangial scales inconspicuous to conspicuous, 0.5–1 mm, lanceolate, with marginal processes, brown.

Distribution and elevation. *Elaphoglossum peltatum* f. *peltatum* occurs in Belize, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, Guadeloupe, Guatemala, Guyana, Haiti, Honduras, Jamaica, Martinique, Mexico, Nicaragua, Panama, Peru, Puerto Rico, and Venezuela. The form has been collected at elevations of (0)1000–3000 m.

Discussion. *Elaphoglossum peltatum* f. *peltatum* is characterized by sterile laminae that are generally dichotomously divided three to seven times, the segments linear and 0.5–2.2 mm wide. It is the most common and widespread form of *E. peltatum* and the only form of the species in the West Indies. *Elaphoglossum peltatum* f. *foeniculaceum* is based on specimens with narrower lamina segments (Figs. 8J, 13P–S). It is most common in Ecuador, but individuals with intermediate segment widths also occur in Ecuador, making it difficult to separate this form from typical form *peltatum*. For this reason, forma *foeniculaceum* is placed here in synonomy.

Additional specimens examined. BELIZE. **Cayo:** in forest along ridge, near ridge top camp in vic. of Doyle's Delight, S Maya Mtns., *Allen 15275* (MO, NY, UC). **Toledo:** S Maya Mtns., Bladen Nature Reserve, large sinkhole just S of upper Bladen Branch & 1.3 airline km SE of "AC Camp," *Davidse et al. 35900* (BRH, MO); Maya Mtns., Bladen Nature Reserve, Upper Bladen, Branch basin, along main Bladen canyon, *Holst et al. 5517* (BRH, MO, UC).

BRAZIL. **Amazonas:** N massif plateau of Serra Araca, *Prance et al. 29196* (NY); betw. Missâo Salesiana & Serra Pirapucú, *Silva & Brazâo 60851* (NY, UC). **Bahia:**

Camacan, Res. Serra Bonita, 9.7 km W de Camacan, *Matos 1330* (NY); Camacan, Faz. Serra Bonita, Reserva Serra Bonita, 9.7 km W de Camacan na estrada para Jacarecí, dai 6 km SW na estrada para RPPN Serra Bonita e Torre da Embratel, *Matos & Santos 1584* (NY). **Minas Gerais:** Mpio. Conceição, Serra do Cipó, Km. 152 estrada de Conceição, *Barreto 8851* (GH, RB). **Rio de Janeiro:** Itatiaia, Taquaral, *Campos-Porto 2645* (RB).

COLOMBIA. **Antioquia:** Mpio. Dabeiba, 32 km SE de Mutatá en la vía Mutatá–Dabeiba, río Chever, sitio Chever, *Callejas et al. 5076* (COL, MO, NY); Río Chiado, 65 km S of Turbo, *Haught 4638* (COL, NY); Mpio. Briceño, Correg. San Fermín, finca de los Montoya, 2 km de la vía que de Ventanas conduce a Briceño, *Vasco et al. 459* (HUA, NY). **Bolívar:** Boca Antizales, on Río Esmeralda, *Pennell 4486* (NY), *4507* (NY). **Boyacá:** Mpio. de Sta. María, vía Sta. María-Mambita, trayecto desde el río Garagoa a Sta. María, *Fernándes-Alonso et al. 24771* (COL); Mpio. Sta. María, vereda Calichana, sendero Ecol. Hyka-Quye, *González et al. 579* (COL, NY). **Caquetá:** Mpio. San Vicente de Caguán, transecto Neiva–San Vicente del Caguán, cerca de Los Andes, arriba del río Pato, *Churchill et al. 16890* (NY). **Cauca:** Mpio. de el Tambo, Reserva Nat. Tambito, *Casañas 252* (COL); Mpio. Guapi, Par. Nac. Isla Gorgona, camino hacia el mirador, *Fernández & Fuertes 278* (COL, NY). **Cesar:** Sierra Perijá, *Haught 4494* (COL, NY). **Chocó:** Carr. Yuto–Lloró, 1 km de Yuto, *Forero & Jaramillo 2709* (COL, MO, NY); rd. to Llora from Yuto, along creek ca. 2 km E of Yuto, *Gentry & Renteria 24416* (COL, MO); Nuquí, Alto de Buey, *von Sneidern A.38* (AAU, GH); Cabo Corrientes, Río Parguera, at foot of Janano Mt., *Warner 298* (COL, MO, NY). **Cundinamarca:** San Antonio Valley, 15 km SE of Gutiérrez, 60 km S of Bogotá, *Grant 9809* (COL); Monte Redondo, *Idrobo 1490* (COL, MO). **Magdalena:** Sierra de Onaca, *Smith 1042* (GH, MO, NY, UC). **Meta:** cordillera La Macarena (extremo NE) macizo Renjifo, *Idrobo & Schultes 1102* (COL, GH); Sierra de la Macarena, central mtns., N ridge, *Philipson & Idrobo 1845* (COL). **Nariño:** Mpio. Mallama, *Ramírez & González 9042* (UC). **Norte de Santander:** región del Sarare, quebrada de La China (afluente del río Cubugón), entre Sta. Librada y El Caraño, *Cuatrecasas 12998* (COL, UC); vic. of Toledo, *Killip & Smith 20095* (GH, NY). **Putumayo:** W of Mocoa, cuesta de Filo do Barniz, highest slope & top of ridge, *Barclay & Juajibioy 9451* (COL, GH, MO); 50 km al W del Pepino, *Hagemann & Leist 1543* (COL). **Risaralda:** Mpio. Mistrató, arriba del río Currumay vía Puerto de Oro, *Orozco et al. 2164* (COL). **Santander:** Mpio. Charalá, correg. Virolín, vereda El Reloj, *Díaz 1306* (COL); Mpio. Charalá, Virolín, *Ohba & Barbosa 75* (MO). **Valle del Cauca:** La Cumbre, cordillera Occidental, *Killip 11618* (GH, NY); Bajo Calima, Concesión Pulpapel/Buenaventura, carr. Canalete, *Monsalve 1798* (MO), *2108* (MO).

COSTA RICA. **Alajuela:** Cantón de Upala, Dos Ríos, 5 km S de Brasiliaargen derecha del río Pizote, *Herrera 1026* (MO); Reserva Biol. Alberto Brenes, N of San Ramón, *Moran 6446* (NY); Cantón de San Ramón, cuenca del San Carlos, ca. Reserva Forestal San Ramón, *Rojas et al. 3893* (MO, NY); Balsa de San Ramón, Stapp farm near school house, *Taylor 17779* (NY). **Cartago:** Cantón de Paraíso, Refugio Nac. Fauna Silvestre Tapantí, newly cut forest trail ca. 2 km beyond bridge adjacent to massive pipeline & ca. 10 km beyond puente Dos Amigos, *Almeda et al. 5807* (GH, MO); Turrialba Volcano, ca. 6 km above Trinidad, *Lent 702* (GH, NY). **Guanacaste:** Cantón de Abangares, La Cruz de Abangares, *Haber & Bello 2870* (MO); Cantón de Liberia, Par. Nac. Guanacaste, cordillera de Guanacaste, Est. Cacão, *Rojas 3031* (NY). **Heredia:** Cantón de Heredia, Vara Blanca de Sarapiquí, N slope of Central cordillera, *Skutch 3132* (GH, NY); 10 km NNE of Heredia, *Tryon & Tryon 7020* (GH, NY). **Limón:** Cantón de Talamanca, Sukut, de las juntas de río Urén y río Sukut 1.5 km aguas arriba sobre éste, margen derecha, *Herrera 3176* (MO); Cantón de Pococi, llanura de Tortuguero, San Juan de Pococi, Cuatro Esquinas, finca de hermanos Rojas Alvarado, *Rojas et al. 1826* (MO). **Puntarenas:** Monteverde, *Palmer 49* (NY); Cantón de Garabito, R. B. Carara, valle del Tarcoles, sector Bijagual, Montañas de Jamaica, *Rojas et al. 1952* (MO); Cantón de Golfito, Est. Río Bonito, Serranias de Golfito, sendero a la toma de agua, siguiendo por la quebrada, *Rojas & Fletes 3185* (MO, NY). **San José:** Cantón de Dota, R. F. Los Santos, cuenca del Savegre, camino a San Gerardo de Dota, orillas de camino, *Rojas 4961* (MO, NY); Cantón de Pérez Zeledón, above Albergue de Montana Savegre, Los Robles trail, near end of 4 × 4 rd., *Ruhfel 4* (CR, GH, INB, USJ).

CUBA. **Granma:** Sierra Maestra, on divide below Loma Joaquin & Punta de Palmamocha, *Ekman 5337* (MO). **Guantánamo:** Baracoa region, *León 12034* (NY); trail Navas to Camp Buena Vista, *Shafer 4461* (GH, NY). **Hologuín:** Sierra de Micaron, on path from Mayari arriba to camp at headwaters, *Ekman 6757* (NY); Camp La Gloria, S of Sierra Moa, *Shafer 8089* (GH, NY). **Santiago de Cuba:** Crest of Sierra Maestra betw. Pico Turquino & La Bayamesa, *Morton & Acuña 3765* (GH, MO, NY, UC); Sevilla estate, near Santiago, *Taylor 539* (NY); Gran Piedra, *Shafer 9021* (GH, NY).

DOMINICA. Betw. Laudat & freshwater lake, *Hodge & Hodge 1784* (GH); Morne Diablotin, *Hodge & Hodge 2803* (GH, NY), *Nicolson 1921* (MO); behind police post at Pont Cassé part way up Morne Trois Pitons, *Lellinger 547* (GH); Laudat, *Lloyd 348* (NY); Mt. Diablotin, *Lloyd 925* (NY).

DOMINICAN REPUBLIC. **Azua:** Santo Domingo, Sierra de Ocoa, San José de Ocoa, Bejucal, slope of Loma de los Palos, *Ekman 11835* (NY). **Barahona:** Montiada Nueva, SE of Polo, *Howard & Howard 8542* (GH, NY); Sierra de Baoruco, 4 km arriba el pueblecito rural de "Entrada de Cortico" en el camino a El Gajo, *Zanoni et al. 18869* (NY). **Distrito Nacional:** Santo Domingo, *Türckheim 2946* (NY). **Independencia:** Sierra de Neiba, along Carretera Internac. near crest of range, along Haitian border, vic. line betw. provinces of San Rafael & Independencia, *Gastony et al. 624* (GH, MO, NY); Sierra de Baoruco, 30 km S of Puerto Escondido en el camino a la Caseta No. 1 de Foresta y E en el camino a Charco Colorado, *Zanoni et al. 33996* (NY). **La Vega:** La Ciénaga, S bank of Río Los Guanos, just above confluence with Río de la Izquierda, *Gastony et al. 240* (MO, NY); 10.7 km W from autopista Duarte on rd. to arroyo Prieto & El Río, *Mejía & Zanoni 4980* (MO, NY). **Pedernales:** Sierra de Baoruco, 7.2–7.7 km S of ridge top, 4.8–5.3 km N of Los Arroyos on Jimaní–Pedernales rd., *Mickel et al. 8956* (MO, NY, UC); Sierra de Baoruco, Sapotén, 5 km S del puesto militar de El Aguacate en la Carretera Internac. a Los Arroyos y Pedernales, *Zanoni et al. 27128* (NY). **Peravia:** cordillera Central, Los Cateyes, falda NE de la Loma Valvacoa, NW de Baní, *Mejía & Pimentel 18355* (MO, NY); cordillera Central, 10 km de Rancho Arriba en la carretera a Piedra Blanca y 4 km en el camino a Mahoma y río Mahoma, "La Colonia" zona rural, *Zanoni et al. 22699* (GH, MO, NY). **Santiago:** Distr. San José de las Matas. Jicomé, arroyo La Guasimita, *Valeur 348* (MO, NY); cordillera Septentrional, sobre la cima de la

Loma Diego de Ocampo (NE de Santiago), *Zanoni et al. 42777* (NY). **Santiago Rodríguez:** cordillera Central, Par. Nac. J. C. Ramírez, entre Monte Llano y Los Descansaderos, *Zanoni & García 41983* (MO, NY).

EL SALVADOR. **Chalatenango:** Los Esemiles, *Yuncker 1125* (UC). **Morazán:** El Zancudo, *Seiler 993* (NY). **Santa Ana:** Par. Nac. Montecristo, cordillera de Metapán, betw. Los Planes & main rd. to mtn. summit, cloud forest just below summit of Montecristo, *Davidse et al. 37298* (BM, ITIC, LAGU, MO); Mpio. Metapán, bosque Montecristo, *Seiler 97* (MO).

ECUADOR. **Azuay:** Hwy. Cuenca-Cola de San Pablo, Contego encamp., *Boeke & Loyola 1015* (NY). **Cañar:** betw. Quillallpa & Kirpud, *Fagerlind & Wibom 713* (MO, S). **Carchi:** Lita, collections made in front of bulldozers constructing the Lita–San Lorenzo rd., 5 km from Lita, *Barfod et al. 41358* (AAU, MO, QCA, QCNE); above San Marcos de los Coaiqueres, on trail toward Gualpí Bajo, *Øllgaard et al. 57380* (AAU, MO, NY, QCA, QCNE). **Cotopaxi:** Quevedo–Latacunga rd., Km. 46 from Quevedo, NE slopes, *Holm-Nielsen et al. 2915* (AAU, MO, NY, QCA); Quevedo–Latacunga rd., *Holm-Nielsen et al. 2944* (AAU, NY, MO, QCA). **Esmeraldas:** Parroquía de Concepción, Playa Rica, *Mexia 8456* (B, GH, MO, S, UC). **Imbabura:** vic. Río Verde, ca. 5 km SW from village of Maní, Río Cachaco, *Sperling & Bleiweiss 5018A* (GH). **Morona-Santiago:** Los Tayos, *Argent & Burbidge 94* (QCA); E slope of cordillera, valley of Ríos Negro & Chupianza, on trail from Sevilla de Oro to Mendez, betw. Hac. Chontal & Sta. Elena, *Camp E-810* (NY). **Napo:** Cantón Mera, hac. La Mascota, *Mexia 7023A* (GH, UC); ca. 50 km NE of Baeza, Cascada de San Rafael, along Río Quijos, *Moran et al. 7565* (NY, QCA, QCNE, UC); rd. Baeza–Tena, 6.8 km from Baeza, *Øllgaard 99983* (AAU, QCA, QCNE). **Pastaza:** rd. N of Mera, toward Río Anzu, Km. 67, *Øllgaard & Navarrete 105643* (AAU, QCA). **Pichincha:** Hotel Tinalandia, 20 km E of Sto. Domingo de Los Colorados, *Balslev & Steere 3230* (AAU, NY, QCA); rd. Quito to Puerto Quito, Km. 113, forest reserve of ENDESA ca. 10 km N of main rd., *Balslev et al. 4688* (AAU, NY, QCA, QCNE, UC); Reserva Maquipucuna, sendero autoguiado, *Vasco et al. 855* (NY, QCA, QCNE). **Tungurahua:** Río Verde, *Lugo 1791* (AAU, GH, MO, NY). **Zamora-Chinchipe:** near Zamora, E slope of Andes, *Knight 686* (GH); Shaime, at jct. of Río Nangaritza & Río Numpatakai, *Øllgaard 98437* (AAU, QCA, QCNE); Cantón Nangaritza, Río Nangaritza, Pachicutza, *Palacios & Neill 6482* (MO, QCNE); area of Est. Cientifica San Francisco, rd. Loja–Zamora, ca. 35 km from Loja, *Werner 687* (MO, NY).

GUADELOUPE. bois du Haut Matouba, *Duss 4147* (NY).

GUATEMALA. **Alta Verapaz:** Mpio. Cobán, Chicu'sha'b [Chicuxab], 8 km al SW de Cobán, *Tenorio et al. 14728* (MO); Coban, *Türckheim 157* (GH, NY, UC); Cubilgüitz, *von Türckheim II.1022* (GH). **Baja Verapaz:** along hwy. CA-14 betw. El Progreso & Cobán, 3 mi. S of Purulhá, 17 mi. N of jct. with Hwy. 17 to Salamá & San Jerónimo, vic. km marker 160, *Croat & Hannon 63771* (MO, UC). **Chiquimula:** Volcán Ipala, near Amatillo, *Steyermark 30515* (GH). **Huehuetenango:** Mpio. Barillas, along rd. from Barillas to Malpais, *Christenhusz et al. 5400* (BM, MO). **Izabal:** vic. Exmibal Camp 2 (La Gloria), NW of lake Izabal, *Jones & Facey 3268* (NY); betw. Banera & "La Presa" in Montaña de Mico, *Steyermark 38277* (GH, NY). **Jalapa:** Volcán Jumay, N of Jalapa, *Steyermark 32470* (GH). **Quezaltenango:** Volcán Junil, *Skutch 957* (GH, NY). **Quiché:** Mpio. Uspantán, San Miguel Uspantán, *Heyde & Lux 3216* (GH, MO, NY). **San Marcos:** near Aldea Fraternidad, betw. San Rafael Pie de la Cuesta & Palo Gordo, W-facing slope of Sierra Madre Mtns., *Williams et al. 25734* (NY).

GUYANA. Upper Mazaruni river region, Karowtipu Mtn., *Boom & Gopaul 7497* (NY); Roraima, *Jenman s.n.* (NY); Mt. Roraima, Waruma trail, *Persaud 117* (NY); Mt. Roraima, upper slopes, Rondon Camp, *Tate 505* (NY).

HAITI. Massif du Nord, Port-de-Paix, Haut Piton, *Ekman 4618* (NY); vic. of St. Louis du Nord, mtns. S of town, *Leonard & Leonard 14555* (NY); Savane Zombis, *Pride 136* (GH).

HONDURAS. **Atlántida:** Ravines E of Texiquat river, 1–2 km SW of aldea La Aurora, *Hazlett et al. 8017* (MO). **Choluteca:** Rancho Quemado, Montaña de la Tigra, *Barkley 40047* (GH). **Comayagua:** Mpio. Siguatepeque, summit of San Juanillo, in cordillera de Montecillos Biol. Reserve, *Hawkins & Mejía 529* (MO); Mpio. Siguatepeque, near summit of range above El Achote [Achiote], in cloud zone above plains of Siguatepeque, *Yuncker et al. 6194* (GH, MO, NY). **Cortés:** Mpio. Sta. Cruz de Yojoa, E shore of lake Yojoa, *Williams & Molina 11434* (MO). **Francisco Morazán:** along rd. to Par. Nac. La Tigra, 22–25 km NE of Tegucigalpa, *Croat & Hannon 64055* (MO); Uyuca, *Valerio 759* (GH). **Intibucá:** E of La Esperanza, *Barkley 40355* (GH). **Lempira:** Celaque Nat. Park, trail from Camp 1 to Río Naranjal, *Moran 5556* (MO). **Ocotepeque:** Mpio. Belén Gualcho, cordillera de Celaque, 3 mi. N of Belén Gualcho along rd. to Cucuyagua, *Davidse et al. 35362* (MO). **Santa Bárbara:** 7 km N of El Mochito, on E slopes of Mt. Sta. Bárbara, *Moran 5695* (MO); Mpio. Ilama, Montaña de La Nieve, lado SO del Caserío El Tapiquilar, 20 km S de San Antonio de Cortés [Dept. Cortés on label], *Nelson et al. 8021* (MO). **Sololá**: Volcán Atitlán, *Steyermark 47414* (UC). **Yoro:** Río Pijol Valley, 6 to 7 km S of Nueva Esperanza, *Liesner 26619* (MO); Río Pijol Valley, 7 km SE of Nueva Esperanza, along forested quebrada that flows into Río Pijol & adjacent slopes, *Liesner 26629* (AAU, MO, NY, UC).

JAMAICA. **Portland:** valley of Trafalgar river, near Jumbe Spring, *Maxon & Killip 778* (GH, NY); near Vinegar hill, *Maxon & Killip 828* (GH, NY). **St. Andrew:** trail along leeward slope of Mt. Caledonia, NW of Hardware Gap, *Anderson 3300* (GH); near Hardware Gap, *Harris 10125* (NY), *Yuncker 18489* (NY). **St. Thomas:** Cuna Cuna Gap, *Britton 974* (NY).

MARTINIQUE. Bois des Deun-Choux, *Duss 1617* (NY); bois de la Fontaine, *Hahn 701* (GH); Morne Calebasse, N of Morne Rouge, *Proctor 21735* (GH).

MEXICO. **Chiapas:** Cascada, Siltepec, *Matuda 5122* (GH); Mpio. de Escuintla, Mt. Pasitar, *Matuda S-210* (GH, NY); near Tumbalá, *Nelson 3351* (GH, NY). **Guerrero:** Pilas-Pasión, Distr. Montes de Oca, *Hinton & Hinton 10756* (GH, MO, NY); Teotepec, *Hinton & Hinton 14273* (GH, MO, NY). **Hidalgo:** Mpio. Tlanchinol, 4 km E de Tlanchinol, camino a Apantlasol, *Martínez-Salas 28474* (NY); barranca below Honey Station, *Pringle 10304* (GH, MO, NY, UC). **Jalisco:** Sierra de Manantlán, 15–20 mi. SE of Autlán, on bajada S & W of divide betw. Aseradero San Miguel Uno & Durazno, *McVaugh 13925* (NY); steep mtns. 11–12 mi. S of Talpa de Allende, headwaters of a W branch of Río de Talpa, *McVaugh 21333* (MO, NY). **Oaxaca:** Mpio. de Coicoyán, Siki Nami, SW de Coicoyán, *de Avila 728* (MO, NY); Mpio. San Miguel Chimalapa, cerro Guayabitos, ca. 42 km en línea recta al N de San Pedro Tapanatepec, al NO de la Congregación Benito Juárez, filo alto al SE de la cima, *Wendt et al. 5185* (NY). **Puebla:** La Unión, 12 km NE

de Tlatlauqui, carretera a Mazatepec, *Tenorio 14278* (NY); Mpio. de Teziutlán, Agua de Obispo, *Ventura-A 13637* (NY). **Veracruz:** Mpio. de Catemaco, Cumbres del Bastonal, NW de Tebanca, *Cedillo 3321* (GH, NY); Mpio. de Soteapan, base of Volcán Sta. Marta, 0–3 km E of village of Sta. Marta, *Nee et al. 24657* (NY); Mpio. de Atzalan, Cañada de Tatzayanalan, *Zamudio & Zamora 8466* (NY).

NICARAGUA. **Atlántico Norte:** Mpio. de Siuna, Reserva Bosawas, sendero rumbo a la cara oeste del cerro Saslaya, *Rueda et al. 4384* (HULE, MO); Mt. Livico, Madregava, *Seymour 3088* (F, GH, MO). **Atlántico Sur:** ca. 1 km N of El Zapote, 6 km S of Colonia Verdún, *Nee & Vega 27922* (MO); along new rd. from Río Blanco to Río Copalar, ca. 31 km E of Río Blanco, *Stevens 12166* (MO). **Estelí:** cerro Quiabú, 8 km al NW de Estelí, *Grijalva & Araquistain 595* (MO, NY, UC); ca. 23.5 km (by rd.) NE of Hwy. 1 at Estelí & ca. 2.8 km SE of Laguna Miraflores, *Henrich & Stevens 411* (MO, NY). **Granada:** Volcán Mombacho [Seymour series], *Atwood 3913* (MO, NY, UC); upper slopes of Volcán Mambacho, along W shore of lake Nicaragua, ca. 15 km S of Granada, *Croat 39143* (MO); Mombacho Volcano, *Maxon et al. 7794* (GH, US). **Jinotega:** Reserva Nat. Kilambé, Mpio. de Bocay, Comun. Sta. Teresa de Kilambé, *Rueda et al. 15532* (HULE, MO); mtns. betw. Matagalpa & Jinotega, cordillera Central de Nicaragua, *Williams et al. 23461* (MO, NY). **Matagalpa:** Falda NO del cerro Musún, al lado del río Bilampí, 4 km SO de Wanawás, *Araquistain & Moreno 2611* (MO, NY, UC); Sta. María de Ostuma, *Neill 863* (MO). **Nueva Segovia:** Mpio. de Jalapaontaña, cerro de Jesús, *Paguaga & Toval 19* (HULE, MO). **Río San Juan:** Mpio. el Castillo, Reserva Indio-Maíz, a lo largo del río Bartola entre el caño la Largarta y la cabecera del río Bartola, *Rueda et al. 5124* (HULE, MO); Mpio. el Castillo, Reserva Indio-Maíz, a lo largo del Caño Chontaleño, *Rueda et al. 5802* (HULE, MO); Mpio. el Castillo, Reserva Indio-Maiz, cerro el Diablo, *Rueda et al. 9701* (HULE, MO).

PANAMA. **Bocas del Toro:** Camp. Lucho, *Alfaro & Monro 5608* (MO); Fortuna Dam area, Cont. Divide, ridge trail to unnamed peak to E of Oleoducto rd., *Churchill 5865* (MO). **Chiriquí:** Distr. Boquete, Palo Alto, 4.5 mi. NE of Boquete, in forest along trail toward cerro La Trompeta, *Hammel 7477* (MO, PMA); Cerro de Lino, above El Boquete, *Maxon 5219* (GH, NY); Valley of upper Río Chiriquí Viejo, vic. Monte Lirio, *Seibert 173* (GH, MO, NY). **Coclé:** Bismark, above Penonomé, *Williams 504* (NY); betw. Las Margaritas & El Valle, *Woodson Jr. et al. 1252* (GH, MO, NY). **Colón**: Dto. Donoso, *Clark 12471* (UC). **Darién:** Cerro Pirre, *Duke 13847* (NY); Cana & vic., *Williams 899* (NY). **Panamá:** Altos del Castillo, cerro Azul, a 15 km de la carretera principal, *Casal 28a* (MO, PMA); 2–3 mi. S of Goofy Lake, rd. to Cerro Jefe, *Lewis et al. 293* (GH, MO, UC).

PERU. **Amazonas:** Condorcanqui, Río Cenepa region, near Shaim above quebrada Nahim, one-day walk from Huampami, *Berlin 445* (AAU, MO); Bagua, Dto. Imaza, Comun. Yamayakat, *Rojas et al. 548* (MO, NY, UC); Bagua, Montenegro–Chiriaco, *Sagastegui 5932* (GH). **Junín:** Prov. Satipo, Gran Pajonal, near Chequitavo, *Smith & Rutter 6671* (MO, NY); Satipo, Gran Pajonal, E of Chequitavo on trail to Kotampaz, *Smith 6772* (MO, UC). **Loreto:** Coronel Portillo, Km. 209 entre Tingo María y Pucallpa, Aguaytía, *Ridoutt s.n.* (GH); Coronel Portillo, Distr. Padre Abad, Boquerón de Padre Abad, *Schunke-Vigo 3047* (COL, GH, NY). **Pasco**: Dto. Palcazú, *Vasquez et al.* 29558 (UC). **San Martín:** Rioja, Venceremos, Km. 391 Bagua–Moyobamba rd., *Smith et al. 5959* (MO). **Ucayali:** Boquerón Pass, 92 km from Tingo María on hwy. to Pucallpa, *Allard 22122* (GH).

PUERTO RICO. cordillera Central, Toro Negro State Forest, along headwaters of Río Inabón above high falls, *Proctor 40076* (NY); Caribbean Natl. Forest, slopes of El Yunque, *Scamman 6545* (GH); near Mt. Jajuya, 2 Jan. 1978, *Tullis s.n.* (GH); Luquillo Mtns., *Wilson 76* (GH, NY).

VENEZUELA. **Amazonas:** Dpto. Río Negro, Camp XI, Cerro de la Nebilna, 6.2 km NNE Pico Phelps [Neblina], 20.5 km ENE Neblina Base Camp, along stream Caño Beitel, S of camp, *Beitel 85271* (MO, NY, UC); Mpio. Atabapo, Cerro Marahuaca, "Sima" area, *Liesner 25076* (MO, NY, UC). **Aragua:** along rd. betw. Maracay & Ocumare, Henri Pittier Nat. Park, at summit in cloud forest zone, *Croat 60591A* (MO); Par. Nac. Henry Pittier, trail above Guamitas to summit of La Mesa, above El Limón, *Steyermark 89823* (GH). **Barinas:** Distr. Bolívar, La Soledad, *Ortega 1203* (MO, NY); rd. from Santo Domingo to Barinitas, quebrada on rocks, *Wessels-Boer 1994* (MO). **Bolivar:** Mt. Roraima, SW-facing quebrada near Rondón Camp, *Steyermark 58694* (GH, NY); Ptari-tepuí, steep S-facing slopes, betw. "Cave Rock" & base of high sandstone bluffs, *Steyermark 59580* (GH, MO, NY). **Falcón:** Sierra San Luis, ca. Hotel Parador, *Wingfield & van der Werff 6560* (MO), *6586* (MO, UC). **Lara:** Jiménez, Par. Nac. Yacumbu, *Quijada 121* (NY); Palavecino, fila de Terepaima, betw. Alto de Chuparral & Loma Redonda, 21–23 km S of Cabudare, *Steyermark et al. 103394* (NY). **Mérida:** Canagá y Mucuchachí, Distr. Arzobispo Chacón, *Ruiz-Terán & Lopez-Figueiras 655* (NY); betw. Mucuchachí & Canaguá, *Steyermark 56334* (GH, MO). **Portuguesa:** Depto. Guanare, ESE of Paraísco de Chabasquén, along rd. to Cordoba, ca. 20–25 min. from Chabasquén, *Smith et al. 1004* (MO); selva nublada, 15 km. E de Chabasquén, 67 km. NNO de Guanare, *Steyermark et al. 126574* (MO, UC). **Sucre:** Península de Paria, Cerro de Humo, a lo largo de las cabeceras del río Sta. Isabel, acerca de camino de bestias entre "Los Positos" y La Roma, *Steyermark 96335* (GH). **Táchira:** Cerro Las Minas, bordering quebrada Las Minas, 18 km SE of Sta. Ana, *Steyermark & Liesner 118993* (MO, NY); Distr. Uribante, Empresa Las Cuevas near La Fundación, *van der Werff & González 5032* (MO). **Yaracuy:** Sierra de Aroa, cerro Negro, arriba de San Felipe, *Steyermark & Wessels-Boer 100452* (NY); Carretera entre Buenos Aires y Guamales, parte occidental de la Sierra de Aroa, Distr. Urachiche, N de Urachiche, *Steyermark et al. 114074* (NY).

13c. Elaphoglossum peltatum (Sw.) Urb. f. **standleyi** (Maxon) Mickel, Brittonia 32: 116. 1980. Basionym: *Rhipidopteris standleyi* Maxon, Amer. Fern J. 18: 1. 1928. *Peltapteris flabellata* f. *standleyi* (Maxon) C. V. Morton, Amer. Fern J. 45: 13. 1955. TYPE: Costa Rica. San José: near La Hondura, [10°04″N, 83°59″W], 1300–1700 m, 2–4 Mar. 1924, *P. C. Standley 36464* (holotype, US!). Figures 8F, 13A–C.

Rhizomes 1–2 mm wide, long-creeping; rhizome scales 1.5–4 mm, spreading to appressed, lanceolate, entire or nearly so, light orange to brown, dull. Sterile leaves 2–3.8 cm; petioles 1 to 1.3 times the lamina length; petiolar scales 1–2 mm, clasping to slightly

spreading, ovate to narrowly lancolate, with marginal teeth or processes toward the base, brown, dark at the point of attachment; laminae 0.8–1.6 × 0.9–2.8 cm, ca. as long as wide, chartaceous, simple, circular to flabellate or lunate, minutely crenulate on distal margins, apices broadly obtuse, rarely notched, bases broadly cuneate; adaxial lamina surface scaly, the scales 0.5–1 mm, ovate to narrowly lanceolate, light brown; abaxial lamina surface with scales like those adaxially. Fertile leaves 3–3.4 cm; petioles 4 to 6 times the lamina length; laminae 0.5–0.7 × 0.5–1 cm, circular or slightly lobed, margins entire or slightly crenate, apices rounded, bases cordate; intersporangial scales ca. 1 mm, lanceolate, with marginal processes, brown.

Distribution and elevation. *Elaphoglossum peltatum* f. *standleyi* occurs in Colombia, Costa Rica, Ecuador, Panama, Peru, and Venezuela at elevations of 450–2200 m.

Discussion. *Elaphoglossum peltatum* f. *standleyi* is characterized by sterile laminae that are undivided and circular to flabellate or lunate, and fertile laminae that are circular or slightly lobed. Occasionally, apically notched laminae are found along the same rhizome as leaves with entire margins.

Additional specimens examined. COLOMBIA. **Antioquia:** Par. Nac. Nat. Las Orquídeas, sect. Venados, *Cogollo et al. 2917* (COL, MO). **Cundinamarca:** Fasagasugá, *Lindig 270* (GH). **Putumayo:** W of Mocoa, Cuesta de Filo de Barniz, highest slope & ridge top, *Barclay & Juajibioy 9453* (COL, GH).

COSTA RICA. **Alajuela:** Cantón de Upala, cuenca del Zapote, Bijagua, camino a la toma de agua, *Rojas & Soto 4278* (MO, NY); Cantón de San Ramón, N slope of ridge along quebrada draining E to Río Cataratitas, ca. 20 km NW of San Ramón, *Smith et al. 2220* (AAU, MO, NY, UC). **Cartago:** Casa de Tejas Ridge above Río Gato, *Lent 3699* (AAU, NY); Cantón de Turrialba, Res. Biol. Barbilla, cuenca del Matina, camino a valle Escondido, entrando por las Brisas de Pacuarito, entre la casa de Don Felipe Salazar y parte alta de la fila de regreso, *Rojas et al. 5053* (MO, NY). **Guanacaste:** ca. 5 km E of Tilarán, above laguna de Arenal, *Williams & Williams 24575* (MO, NY). **Puntarenas:** Cantón de Coto Brus, P. I. La Amistad, cordillera de Talamanca, Est. Pittier, frente al portón de la entrada del Parque (potrero), *Angulo 364* (MO); Monteverde, Quaker Colony, *Hauke 477* (NY). **San José:** Cantón de Moravia, along Río Hondura, where Río Zurquí flows into Río Hondura, below bajo La Hondura, *Taylor & Taylor 11943* (MO, NY).

ECUADOR. **Carchi:** San Marcos de los Coaiqueres, on trail Chical-Tobar Donoso, *Øllgaard et al. 57642* (AAU, NY). **Esmeraldas:** Rd. Lita-Urbina, Km. 38.8, *Øllgaard et al. 98682* (AAU, QCA, QCNE). **Morona-Santiago:** cordillera de Cutucú, W slopes, along trail from Logroño to Yaupi, *Madison et al. 3313* (GH); trail along Río Inimkis, ca. 3 km NE of village of Inimkis (San Luis) toward foothills of cordillera Cutucú, *Øllgaard & Navarrete 1433* (QCA). **Napo:** Shell-Mera, *Asplund 19710* (NY). **Pastaza:** E of Puyo, along rd. to Macas, around Mpio. Stadium, *Fay & Fay 3604* (MO, NY, QCNE); Shell-Mera forest, 2 km N of Shell-Mera, *Holm-Nielsen & Jeppesen 425* (AAU, S); Puerto Santana, 20 km along Río Pastaza, SSE of Shell-Mera, *Holm-Nielsen & Jeppesen 532* (AAU, GH, S). **Tungurahua:** Río Negro, just outside village, *Fagerlind & Wibom 1255* (MO, S); vía Baños–Puyo, sendero que conduce al río Cristal, *Pérez & Moscoso 2702* (QCA).

PANAMA. **Bocas det Toro:** betw. Fortuna Dam and Chiriquí Grande, *Croat & Grayum 60433* (UC). **Coclé:** Vic. El Valle, *Allen 1260* (GH, MO, NY); betw. Cerro Pilón & el valle de Antón, *Baker 13961* (NY); 3-mtn. ridge above El Valle, *Hamilton et al. 4122* (AAU, MO, UC). **Panamá:** sendero de interpretación, 1 km E del camp. de los guardabosques de INRENARE, *Correa et al. 8044* (PMA); Par. Nac. Altos de Campana, sendero de interpretación, *Correa et al. 8577* (NY). **Veraguas:** Distr. Sta. Fé, NW of Sta. Fé, 8.8 km from Escuela Agricola Alto de Piedra, Pacific slope, *Mori et al. 3984, 3998* (MO, WIS).

PERU. **Cusco:** Paucartambo, Pillawata, Yanamago–Tambomayo, *Vargas-Calderón 16733* (GH).

VENEZUELA. **Aragua:** river Tuy below Colonia Tovar, *Fendler 263* (GH, MO, NY, YU).

14. Elaphoglossum rhomboideum A. Vasco, Mickel & R. C. Moran, sp. nov. TYPE: Ecuador. Carchi: valle de Maldonado, Km. 67 on rd. Tulcán–Maldonado, 0°53″N, 78°04″W, 2400 m, 20 Mar. 1973, *L. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B. Øllgaard 6168* (holotype, AAU!; isotypes, MO!, UC!). Figures 5G–J, 11E–J, 12.

Rhizomes 1 mm wide; rhizome scales 3–4 mm, appressed, lanceolate, entire, light orange to brown, concolorous or with dark point of attachment, dull. Sterile leaves 2.4–4.7 cm; petioles 0.7 to 3.3 times the lamina length; petiolar scales 2–2.5 mm, scattered, lanceolate, entire, light orange to brown, concolorous; laminae (0.7–)0.9–1.6 × 0.9–1.9 cm, 0.8 to 1 times longer than wide, chartaceous, simple, rhombic to (less commonly) triangular, margins minutely crenulate, apices rounded to broadly acute, bases broadly cuneate or (in triangular laminae) truncate; adaxial surface with scales 1–2 mm, brown, ovate to lanceolate, often hastate at the base; abaxial lamina surface with scales 1–2 mm, brown, ovate to lanceolate, often hastate at the base. Fertile leaves 2.7–7.5 cm; petioles 2 to 3 times the lamina length; laminae 0.7–1 × 0.6 cm, broadly ovate, entire, apices rounded, bases broadly cuneate; intersporangial scales 1.5–2 mm, hastate with lateral processes, brown, shiny.

Etymology. *Elaphoglossum rhomboideum* is characterized by small rhombic leaves, thus the specific epithet from the Latin.

Distribution and elevation. *Elaphoglossum rhomboideum* is known only from the border areas between

Colombia and Ecuador, on the western side of the Andes, and has been collected at elevations from 2400 to 3200 m.

IUCN Red List category. Because *Elaphoglossum rhomboideum* is a new species, more information is needed to determine its appropriate IUCN listing. Therefore it should be included in the category Data Deficient (DD), according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Elaphoglossum rhomboideum* is characterized by small rhombic laminae and resembles *E. andreanum* in its small size, crenulate lamina margins, and geography, but that species differs by more elongate triangular laminae. Another difference is the tendency for *E. rhomboideum* to have brown, concolorous laminar scales, whereas those of *E. andreanum* are typically black or at least dark at the point of attachment. Some *E. concinnum* specimens with rhombic leaves might resemble *E. rhomboideum*, but *E. concinnum* is known only from southern Ecuador and northern Peru (Fig. 1C), whereas *E. rhomboideum* is so far known only from the western side of the Andes in southern Colombia and northern Ecuador (Fig. 12).

Paratypes. COLOMBIA. **Cauca:** above Carpintero, E Slope of W cordillera, [2°47″N, 76°36″W], 2500 m, 23 Apr. 1939, *A. H. G. Alston 8235* (MO); Par. Nac. Nat. Munchique, [2°42″N, 77°05″W], 2800 m, *F. González 3116* (COL, NY); Cerro de Munchique, [2°32″N, 76°59″W], 2400 m, Mar. 1884, *F. C. Lehmann 3641* (K).

ECUADOR. **Carchi:** valle de Maldonado, Km. 67 on rd. Tulcán–Maldonado, 0°53″N, 78°04″W, 2400 m, 20 May 1973, *L. B. Holm-Nielsen, S. Jeppesen, B. Løjtnant & B. Øllgaard 6168* (AAU, MO, UC); rd. Tulcán–Maldonado, 53–54 km from Tulcán, [0°50″N, 78°03″W], 3100–3200 m, 31 July 1976, *B. Øllgaard & H. Balslev 8306* (AAU).

15. Elaphoglossum squamipes (Hook.) T. Moore, Index Fil. 15. 1857. Basionym: *Acrostichum squamipes* Hook., Icon. Pl. 2: tab. 197. 1837. TYPE: Peru. Amazonas: Chacapoyas, [6°13″S, 77°51″W], 1836, *Mathews s.n.* (holotype, K!; isotype, NY!). Figures 2N–Q, 3A–F, 6D, 10A–D.

Acrostichum ovatum Liebm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 5. 1: 164. 1849, nom. illeg., non *Acrostichum ovatum* Hook. & Grev., 1831 nec *Acrostichum ovatum* Fée 1872. Replacement synonym: *Elaphoglossum subaequale* T. Moore, Index Fil. 368. 1862. TYPE: Mexico. Oaxaca: slopes of Cerro Zempoaltépetl, [17°25″N, 95°58″W], 2660–3000 m, June 1842, *F. Liebmann s.n.* [Pl. Mex. 2431, Fl. Mex 5] (holotype, C!; isotypes, B-20 0072019d!, K!, K fragm. US!).

Elaphoglossum craspedariiforme (Fée) Brade ex Alston, Bol. Soc. Brot. sér. 2, 32: 26. 1958, as "craspedariaeforme." Basionym: *Acrostichum craspedariiforme* Fée, Crypt. Vasc. Brésil. 1: 261. tab. 81, fig. 1. 1869. TYPE: Brazil. Rio de Janeiro: Serra dos Orgãos, [22°26″S, 42°59″W], 8 Aug. 1869, *A. F. M. Glaziou 3550* ["*3350*" sic, protologue] (holotype, P! [2], P photos MO!, NY!; isotypes, B!, K!).

Rhizomes 1–2 mm wide; rhizome scales 3–4.5 mm, appressed, ovate to linear or lanceolate, entire, light orange, dull. Sterile leaves 4.5–16.5 cm; petioles 0.75 to 2.2 times the lamina length; petiolar scales 2–3 mm, slightly spreading, ovate to narrowly lanceolate, entire or occasionally with marginal processes at the base, light orange to brown, concolorous; laminae 3–12.5 × 0.8–2 cm, 1.8 to 2.5(to 4) times longer than wide, coriaceous, simple, ovate-lanceolate or spatulate, entire to occasionally (especially in small leaves) minutely crenulate, apices obtuse, bases broadly cuneate; adaxial lamina surface scaly, the scales 0.5–2.5 mm, linear to hastate, often coarsely and irregularly toothed, especially toward the base, light brown to brown, often darkened at point of attachment and centrally; abaxial lamina surface with scales like those adaxially. Fertile leaves 3.2–12.5 cm; petioles 2.8 to 4.5 times the lamina length; laminae 0.7–2.5 × 0.5–1.1 cm, ovate to elliptic, entire, apices obtuse, bases slightly cordate to short-decurrent; interspangial scales 1–2 mm, marginal processes occasionally present, light brown to dark brown.

Distribution and elevation. *Elaphoglossum squamipes* is distributed in Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Panama, Peru, and Venezuela. It has been collected at elevations of (800–)1700–3930 m.

Discussion. *Elaphoglossum squamipes* is characterized by petioles 0.7 to 2.2 times longer than laminae, laminae generally entire, ovate-lanceolate or spatulate with obtuse apices, and laminar scales light brown to brown. Although not constant, most specimens of *E. andreanum* differ from *E. squamipes* by the laminae with minutely crenulate margins and mostly dark brown scales. General leaf shape is very similar in some specimens of *E. squamipes* and *E. lloense*. *Elaphoglossum squamipes* differs by smaller leaves (3–12.5 cm vs. 6–25 cm in *E. lloense*), somewhat narrower laminae (0.8–2 cm vs. 1.1–2.8 cm), and obtuse lamina apices (vs. attenuate). *Elaphoglossum minutum* might be confused with *E. squamipes* because of their similar general leaf shape, but *E. minutum* differs by its presence at lower elevations (100–1000[–1700] m vs. [800–]1700–3930 m in *E. squamipes*) and more oblong, often parallel-sided laminae.

Our unpublished molecular phylogenetic studies based on chloroplast markers (*atpB-rbcL*, *rps4-trnS*, and *trnL-F*) resolved the Brazilian accesions of *Elaphoglossum squamipes* in a different clade distinct from the other accessions of *E. squamipes* from elsewhere. We cannot, however, find any morphological characters to distinguish these two clades, and therefore we will continue to recognize the Brazilian and non-Brazilian plants as the same species. If the disjunct populations in southeastern Brazil were to be recognized as taxonomically distinct, the name *E. craspedariiforme* would apply.

Additional specimens examined. BOLIVIA. **Cochabamba:** Prov. Carrasco, 100 km antigua carr. Cochabamba-Villa Tunari, *Kessler et al. 6742* (UC). **La Paz:** Prov. Franz Tamayo, bajando por el sendero al frente de Puina (pueblo antiguo), río abajo, *Jiménez et al. 2888* (LPB, MO, UC).

BRAZIL. **Minas Gerais:** Boacaina de Minas, Par. Nac. Itatiaia, Alto dos Brejos, *Condack 250* (RB), *Condack 318* (RB). **Rio de Janeiro:** Itatiaya, *Brade & Tamandaré 6447* (GH, NY, RB, UC); Bananal, *Brade 15206* (RB); Itatiaia, *Brade 15531* (F, GH, MO, NY, RB); Itatiaia, Par. Nac. Itatiaia, Maromba, trilha para o Véu da Noiva, *Sylvestre et al. 1878* (RB). **São Paulo:** Santo André, Alto da Serra, *Brade 5290* (AAU, GH, NY, RB, UC); Rio Grande, *Wacket 301* (K, NY, RB, UC).

COLOMBIA. **Boyacá:** arriba de la carr. Tunja Arcabuco, quebrada afluente del río Pómeca, *Jaramillo-M. et al. 3678* (COL, NY); Mpio. Villa de Leyva, SFF de Iguaque, bosques secund. de Robles, ca. al centro de visitantes, *Vasco et al. 759* (HUA, NY). **Magdalena:** Sierra Nevada de Sta. Marta, transecto del Alto Río Buriticá, *Jaramillo-M. et al. 5355* (COL). **Norte de Santander:** La Mesita, Pamplona, *Alston 7201* (COL, F, NY). **Quindío:** Mpio. de Génova, camino finca Servia, *Vélez et al. 1820* (COL). **Santander:** W slope of Páramo Rico, *Killip & Smith 17748* (GH). **Tolima:** Mpio. de Sta. Isabel, cordillera Central, vertiente oriental, valle del río Totarito, *Jaramillo-M. et al. 6381* (COL).

COSTA RICA. **Cartago:** Cantón de El Guarco, Reserva For. Río Macho, cuenca del Reventazón, Estación Ojo de Agua, sendero La Quebrada, *Gamboa 995* (INB, MO); below crater of Turrialba Volcano, *Lent 717* (GH, NY). **Heredia:** Cantón de Barva, P. N. Braulio Carrillo, cordillera Central, Estación Barva, *Fernández & García 1433* (MO); slopes & ridges above Laguna del Barva & summit of Volcán Barva, *Grayum & Quesada 7431* (MO). **Puntarenas:** Cantón de Coto Brus, Cerro Echandi, Costa Rica–Panama border, Puntarenas–Bocas Prov. border, *Gómez et al. 21843* (AAU, MO); Cantón de Buenos Aires, P. N. La Amistad, Tararia, Limón/Puntarenas, Par. Internac. La Amistad, sendero a cerro Kámuk, entre cerro Kas, *Rojas 3197* (MO, NY). **San José:** Cantón de Pérez Zeledón, Albergue Cuericí, El Sitio, *Moran 6308* (MO, NY); Cantón de Pérez Zeledón, P. N. Chirripó, cordillera de Talamanca, *Rojas 2853* (MO); Cantón de Pérez Zeledón, rd. from Cartago to San Isidro del General (Pan Amer. Hwy., Rt. 2), Km. 96–97, ca. 1.5 km S of Villa Mills, near Siberia, *Smith & Béliz 2050* (MO).

ECUADOR. **Cañar:** N rim of the Río Cañar valley, betw. Suscal & Chontamarca, *Camp E-2882* (F, NY). **Chimborazo:** rd. 10 km NE of Alao, at Cuspipaccha, *Øllgaard et al. 38189* (AAU). **Cotopaxi:** Cantón Sigchos, en la cima del cerro Azul, ca. 1:20 horas de casa del Sr. Marco Sillio, *Ramos et al. 6629* (COL, CUVC, MO, QCNE), *Ramos et al. 6669* (CUVC, NY, QCNE, UC). **Imbabura:** Lago San Marcos, Cayambe, *Cazalet & Pennington 5479* (NY, UC). **Loja:** Par. Nac. Podocarpus, Cajanuma, matrix plot M1, *Lehnert 2259* (QCA). **Napo:** Near Papallacta, Aug. 1918, *Mille s.n.* (GH, NY); Oyacachi, 5 km después del paso, *Navarrete 1356, 1380* (NY, QCA). **Pichincha:** Cerro Pasochoa, *Eriksen 59211* (QCA, QCNE); W of pass betw. Iliniza & Carazón, rd. & trail from Chaupi, *Øllgaard et al. 1185* (AAU, QCA, QCNE). **Tungurahua:** Cantón Santiago de Píllaro, Par. Nac. Llanganates, carr. Píllaro-Represa Pisayambo-líaguna Cochas Negras, camino río Milín-Aucacocha, *Freire et al. 3011* (MO, QCNE); S slope of volcano Tunguragua, *Rimbach 7* (GH, NY).

EL SALVADOR. **Chalatenango:** bosque de El Pital, *Montalvo 4812* (MO); summit of Cerro El Pital, *Seiler 149* (F); Cerro El Pital, *Seiler 745* (GH, NY).

GUATEMALA. **Chimaltenango:** Tecpán, 23 Dec. 1936, *Faull s.n.* (GH); Cerro de Tecpám, region of Sta. Helena, *Standley 60956* (F). **Huehuetenango:** Sierra Cuchumatanes, rd. to San Juan Ixcoy, *Molina 21313* (F).

HONDURAS. **Lempira:** Camino entre la montaña El Mojon y San Manuel de Colohete, Par. Nac. Celaque, *House 1129* (MO); Celaque Nat. Park, betw. Camp 1 & first summit, ca. 8 km WSW of town of Gracias, *Moran 5643* (MO).

MEXICO. **Chiapas:** Motozintla, N & W slope of Cerro Mozotal below microwave tower along rd. from Huixtla to El Porvenir & Siltepec, *Breedlove & Smith 22733* (F, MO, NY); El Porvenir, along rd. betw. Motozintla de Mendoza & Siltepec, 21.5 mi. NW of Motozintla, 1.3 mi. E of El Porvenir, *Croat 47349* (MO). **Guerrero:** 2 km NE of Camp. El Gallo, SW slopes of Cerro Teotepec, *Rzedowski & McVaugh 118* (NY) **Oaxaca:** Mixes, W slope of Cerro Zempoaltepetl to Yacoche, *Mickel 4587* (NY); Mixes, NW slope of Cerro Zempoaltepetl, trail from Yacohe to Totontepec, *Mickel 4649* (NY); Cerro de Malacate, N of Capulalpan, ca. 8 km E of Ixtlán, Ixtlán, *Mickel 5266* (NY). **Veracruz:** Coatepec, Cofre de Perote, entre Mesa de Los Laureles y Tierra Grande, bosque de Niebla, *Cházaro & Castillo 6791* (MO); Orizaba, *Müller 39* (NY).

PANAMA. **Bocas del Toro:** cordillera de Talamanca, 8 airline km NW of peak of Cerro Echandi on Costa Rica–Panama internat. border, *Davidse et al. 25269* (MO); Cerro Fábrega, ca. 1.5 km NW of peak, *Monro et al. 4165* (MO). **Chiriquí:** above El Potrero Camp, Volcán Chiriquí, *Maxon 5327* (GH, NY); vic. of Casita Alta, Volcán de Chiriqui, *Woodson Jr. et al. 958* (GH, MO, NY).

PERU. **Amazonas:** Chachapoyas, Cerros Calla Calla, E side, 10 km above Leimebamba on rd. to Balsas, *Hutchison & Bennett 4753* (F, GH, NY, UC); Chachapoyas, Cerros Calla Calla, W side, 45 km above Balsasid-way on rd. to Leimebamba, *Hutchison & Wright 5825* (F, MO, NY, UC); Chachapoyas, around Molinapampa, *van der Werff et al. 16901* (MO, UC); Chachapoyas, upper slopes of Puma-urcu ESE of Chachapoyas, *Wurdack 692* (F, K, NY, UC). **Cajamarca:** Sallique, Lanchal, La Cocha, *Díaz et al. 9669* (MO, UC). **Cusco:** La Convención, Distr. Vilcabamba, Paltaybamba, Ayangate, *Valenzuela et al. 9124* (CUZ, MO). **Junín:** Muña, *Bryan 526* (F); Mito, *Macbride 3359* (F); Muña, *Macbride 4024* (F). **Pasco:** Oxapampa, Distr. Huancabamba, sect. Sta. Barbara, *Mellado & Ortiz 2680* (NY, UC, USM); Oxapampa, Sta. Barbara, *Smith 8164* (MO, NY). **San Martín:** Prov. Mariscal Cáceres, Río Abiseo Nat. Park, Puerta del Monte, *Young 1997* (NY).

VENEZUELA. **Lara:** Parque Nacional Diníra, *Riina et al. 970* (UC). **Mérida:** trail from La Negrita to Boquerón,

quebrada de las Cañas, *Luteyn et al. 6117* (AAU, NY, UC); Carr. Bailadores a La Grita via El Portachuelo, 3 km del cruce a las porqueras, *Vasco 817* (HUA, VEN, NY). **Trujillo:** Distr. Carache, vía páramo Cendé sitio denominado "Las Cruces," *Rivero & Díaz 1486* (MO, NY).

16. Elaphoglossum tripartitum (Hook. & Grev.) Mickel, Brittonia 32: 116. 1980. Basionym: *Acrostichum tripartitum* Hook. & Grev., Icon. Filic. 1: tab. 118. 1829. *Acrostichum flabellatum* var. *tripartitum* (Hook. & Grev.) Baker, Syn. Fil. (Hooker & Baker) 416. 1868. *Rhipidopteris tripartita* (Hook. & Grev.) Fée, Mém. Foug. 2: 79. 1845. *Peltapteris tripartita* (Hook. & Grev.) C. V. Morton, Amer. Fern J. 45: 14. 1955. TYPE: Ecuador. Esmeraldas: 1660 m, s.d., *W. Jameson s.n.* (holotype, K!; isotype, E!). Figures 8O, P, 12.

Rhipidopteris tripartita var. *subbiternata* Hieron., Hedwigia 48: 273. 1909. TYPE: Ecuador. Pichincha: Mt. Pichincha, near Mindo, [00°20″S, 78°47″W], s.d., *M. A. Stübel 760* (holotype, B!).

Rhizomes 1–1.5 mm wide, long-creeping; rhizome scales 3–5.5 mm, appressed, lanceolate, entire or with a few small projections at base, light orange to brown, dull. Sterile leaves 2.5–8.5 cm; petioles 0.5 to 2.5 times the lamina length; petiolar scales 1–3 mm, slightly spreading, lanceolate or sometimes hastate, entire, brown; laminae 1.2–3 × 1.8–4 cm, about as long as wide, chartaceous, ternate to biternate, deltate, minutely crenulate on distal margins, apices broadly obtuse, bases cuneate; adaxial lamina surface sparsely scaly, the scales 0.5–1.5 mm, filiform (the body 2 or 3 cells wide) to hastate, light to dark brown, dull; abaxial lamina surface scaly, the scales 0.5–1.2 mm, lanceolate to hastate, light to dark brown, sometimes darker at point of attachment. Fertile leaves 4.5–7.5 cm; petioles 3 to 6 times the lamina length; laminae 1–1.5 × 0.8–1.4 cm, trilobed, apices rounded, bases truncate or short-decurrent; intersporangial scales 1–3 mm, lanceolate or hastate, brown.

Distribution and elevation. *Elaphoglossum tripartitum* occurs only on the western side of the Andes in northwestern Ecuador and has been collected from elevations of 1200–3200 m.

Discussion. *Elaphoglossum tripartitum* is the only species of *Elaphoglossum* sect. *Squamipedia* with ternate or (in large leaves) biternate laminae. The basal segments can themselves be tripartite at the apex. This distinctive laminar cutting makes this species one of the easiest to identify in the genus. The species also has filiform to hastate scales on the adaxial surfaces of the leaf laminae, a character that is shared only with *E. blepharis*.

Elaphoglossum tripartitum is a narrow endemic, being found only on the western slopes of the Andes near Quito. A form with somewhat more divided laminae was described from Mount Pichincha as *Rhipidopteris tripartita* var. *subbiternata* Hieron., but intergrades with the typical form and does not deserve nomenclatural recognition (Morton, 1955).

Additional specimens examined. ECUADOR. **Azuay:** above Sayausí at first bridge over Río Tomebamba, *Harling & Andersson 22685* (QCA). **Cotopaxi:** Reserva Otonga, entre Quito y Sto. Domingo ca. de San Francisco de las Pampas, *Nowicki 484, 561* (QCA). **Imbabura:** Cantón Cotacachi, Parroquia García Mareno, cordillera de Toisán, cerro de la Plata, bosque protector Los Cedros, *Clark 7422* (NY); res. Los Cedros, cuchilla sur del río Los Cedros, sendero sobre la casa de Agapó hacia el Mirador, *Endara 259* (QCA). **Pichincha:** Cantón Quito, Río Guajalito Reserve, 10 km W of Chiriboga, Km. 59 on old rd. Quito–Santo Domingo, *Fay & Fay 3164* (AAU, MO, QCA, QCNE); rd. Santo Domingo–Quito, above Tandapi (Cornejo Astorga), *Holm-Nielsen et al. 7083* (AAU, MO, NY, UC); Res. Maquipucuna, sendero principal, *Vasco et al. 852* (NY, QCA).

Excluded Species

Elaphoglossum cardiophyllum (Hook.) T. Moore, Index Fil. 7. 1857. Basionym: *Acrostichum cardiophyllum* Hook., Icon. Pl. tab. 715. 1845. TYPE: Ecuador. Pichincha: Quito, Andes, s.d., *W. Jameson 212* (holotype, K!; isotypes, BM!, LE, not seen).

Elaphoglossum cardiophyllum was previously placed in *Elaphoglossum* sect. *Squamipedia* by Mickel and Atehortúa (1980). It superficially resembles members of the section, such as *E. deltoideum*, in its long-creeping rhizomes, distichous leaf arrangement, and small leaves. But other morphological characters and chloroplast DNA evidence strongly support its placement in *Elaphoglossum* sect. *Elaphoglossum*, not *Elaphoglossum* sect. *Squamipedia* (Rouhan et al., 2004). The laminar scales have marginal processes that end in slightly swollen apical cells—as is typical of *Elaphoglossum* sect. *Elaphoglossum*. Furthermore, unlike other taxa of *Elaphoglossum* sect. *Squamipedia* that lack phyllopodia, *E. cardiophyllum* has phyllopodia present, as seen in other members of *Elaphoglossum* sect. *Elaphoglossum*. The perispore of *E. cardiophyllum* resembles that of species belonging to *Elaphoglossum* sect. *Elaphoglossum*; it is not echinulate as in *Elaphoglossum* sect. *Squamipedia* (Moran et al., 2007). *Elaphoglossum cardiophyllum* belongs to *Elaphoglossum* sect. *Elaphoglossum* (Rouhan et al., 2004).

Elaphoglossum ovatum (Hook. & Grev.) T. Moore, Index Fil. xvi. 1857. Basionym: *Acrostichum ovatum* Hook. & Grev., Icon. Filic. tab. 146. 1829. TYPE: Ecuador. Pichincha: Mt. Cayambe, 2133 m, s.d., *W. Jameson s.n.* (holotype, K!).

Elaphoglossum ovatum was previously placed in *Elaphoglossum* subsect. *Ovata* Christ in *Elaphoglossum* sect. *Squamipedia* by Mickel and Atehortúa (1980). However, molecular phylogenetic results have resolved this species in *Elaphoglossum* sect. *Lepidoglossa* (Rouhan et al., 2004).

Elaphoglossum wrightii (Mett. ex D. C. Eaton) T. Moore, Index Fil. 370. 1862. Basionym: *Acrostichum wrightii* Mett. ex D. C. Eaton, Mem. Amer. Acad. Arts n.s. 8: 194. 1860. TYPE: Cuba. Oriente: "prope Monte Verde," s.d., *C. Wright 965* (holotype, B!; isotypes, BM!, GH!, YU not seen). Figure 15F–J.

Elaphoglossum wrightii was previously placed in *Elaphoglossum* sect. *Squamipedia* by Mickel and Atehortúa (1980). This Cuban endemic greatly resembles members of that section in its long-creeping rhizomes, paired peglike aerophores, lack of phyllopodia, and small leaf size (Fig. 15F–J). However, unlike members of *Elaphoglossum* sect. *Squamipedia*, it lacks minute spines on the perispore (Moran et al., 2007). Our molecular phylogenetic study (Vasco et al., in prep.) using three noncoding chloroplast markers resolved this species outside sequenced accessions for *Elaphoglossum* sect. *Squamipedia*, and the species lies sister to the rest of the entire genus, except for *E. amygdalifolium* (Mett. ex Kuhn) Christ. Given this position on the tree, it is interesting to note in regard to the evolution of epiphytism that *E. amygdalifolium* and *E. wrightii* are the only hemiepiphytes in the genus. *Elaphoglossum amygdalifolium* starts growth on the base of tree trunks and then sends roots downward to the soil, with the stem growing only epiphytically (Lagomarsino et al., 2012); that is, it is a primary hemiepiphyte, sensu Benzing (1990). In contrast, individual plants of *E. wrightii* grow both terrestrially and epiphytically, first starting on the soil and then finding a tree to climb (Josmaily Lóriga, pers. comm.).

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Appendix 1. The Neotropical species of *Elaphoglossum* sect. *Squamipedia* and the countries (or islands) in which they occur.

1. *E. andreanum*: Colombia, Ecuador
2. *E. anthracinum*: Colombia, Ecuador
3. *E. blepharis*: Ecuador
4. *E. bryogenes*: Ecuador
5. *E. colombianum*: Colombia
6. *E. concinnum*: Ecuador, Peru
7. *E. deltoideum*: Ecuador
8. *E. feei*: Dominica, Guadeloupe
9. *E. lloense*: Bolivia, Colombia, Costa Rica, Ecuador, Panama, Peru, Venezuela
10. *E. minutum*: Bolivia, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Jamaica, Mexico, Panama, Peru, Venezuela
11. *E. moorei*: Bolivia, Peru
12. *E. nidiforme*: Bolivia, Ecuador, Peru
13. *E. peltatum*

13a. forma *flabellatum*: Bolivia, Colombia, Costa Rica, Ecuador, Guyana, Panama, Peru, Venezuela

13b. forma *peltatum*: Belize, Brazil, Colombia, Costa Rica, Cuba, Dominica, Dominican Republic, Ecuador, El Salvador, Guadeloupe, Guatemala, Guyana, Haiti, Honduras, Jamaica, Martinique, Mexico, Nicaragua, Panama, Peru, Puerto Rico, Venezuela

13c. forma *standleyi*: Colombia, Costa Rica, Ecuador, Panama, Peru, Venezuela

14. *E. rhomboideum:* Colombia, Ecuador
15. *E. squamipes*: Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, Guatemala, Honduras, Mexico, Panama, Peru, Venezuela
16. *E. tripartitum*: Ecuador

Appendix 2. List of names. Accepted names are listed in boldface.

Acrostichum cardiophyllum Hook., see Excluded Species

Acrostichum craspedariiforme Fée = *Elaphoglossum squamipes*

Acrostichum deltoideum Sodiro = *E. deltoideum*

Acrostichum feei Bory ex Fée = *E. feei*

Acrostichum flabellatum Humb. & Bonpl. ex Willd. = *E. peltatum* f. *flabellatum*

Acrostichum flabellatum var. *bipartitum* Sodiro = *E. peltatum* f. *flabellatum*

Acrostichum flabellatum var. *tripartitum* (Hook. & Grev.) Baker = *E. tripartitum*

Acrostichum lloense Hook. = *E. lloense*

Acrostichum minutum Pohl ex Fée = *E. minutum*

Acrostichum moorei E. Britton = *E. moorei*

Acrostichum peltatum (Sw.) Sw. = *E. peltatum* f. *peltatum*

Acrostichum peltatum var. *potentillifolium* Christ = *E. peltatum* f. *flabellatum*

Acrostichum flabellatum var. *sphenophyllum* Kunze = *E. peltatum* f. *flabellatum*

Acrostichum foeniculaceum Hook. & Grev.

Acrostichum ovatum Hook. & Grev., see Excluded Species

Acrostichum ovatum Liebm. = *E. squamipes*

Acrostichum rampans Baker = *E. minutum*

Acrostichum revolutum Liebm. = *E. minutum*

Acrostichum sphenophyllum (Kunze) Kunze = *E. peltatum* f. *flabellatum*

Acrostichum squamipes Hook. = *E. squamipes*

Acrostichum tripartitum Hook. & Grev. = *E. tripartitum*

Acrostichum wrightii Mett. ex D. C. Eaton, see Excluded Species

Elaphoglossum sect. **Squamipedia** Mickel & Atehortúa

Elaphoglossum sect. *Squamipedia* subsect. *Feeana* Christ = *Elaphoglossum* sect. *Squamipedia*

Elaphoglossum andreanum Christ

Elaphoglossum anthracinum A. Vasco, Mickel & R. C. Moran

Elaphoglossum bangii Christ = *E. moorei*

Elaphoglossum blepharis A. Vasco, Mickel & R. C. Moran

Elaphoglossum bryogenes Mickel

Elaphoglossum cardiophyllum (Hook.) T. Moore, see Excluded Species

Elaphoglossum colombianum (Maxon) Mickel

Elaphoglossum concinnum Mickel

Elaphoglossum craspedariiforme (Fée) Brade ex Alston = *E. squamipes*

Elaphoglossum deltoideum (Sodiro) Christ

Elaphoglossum elegantulum Rosenst. = *E. minutum*

Elaphoglossum ensiforme Mickel = *E. lloense*

Elaphoglossum feei (Bory ex Fée) T. Moore

Elaphoglossum flabellatum (Humb. & Bonpl. ex Willd.) Christ = *E. peltatum* f. *flabellatum*

Elaphoglossum foeniculaceum (Hook. & Grev.) C. Chr.

Elaphoglossum lloense (Hook.) T. Moore

Elaphoglossum macilentum Mickel = *E. minutum*

Elaphoglossum minutum (Pohl ex Fée) T. Moore

Elaphoglossum moorei (E. Britton) Christ

Elaphoglossum nidiforme Mickel

Elaphoglossum ovatum (Hook. & Grev.) T. Moore, see Excluded Species

Elaphoglossum peltatum (Sw.) Urb.

forma **flabellatum** (Humb. & Bonpl. ex Willd.) Mickel

forma *foeniculaceum* (Hook. & Grev.) Mickel = *E. peltatum* f. *flabellatum*

forma *potentillifolium* (Christ) Mickel = *E. peltatum* f. *flabellatum*

forma **standleyi** (Maxon) Mickel

Elaphoglossum peruvianum (L. D. Gómez) Mickel = *E. moorei*

Elaphoglossum rampans (Baker) Christ = *E. minutum*

Elaphoglossum revolutum (Liebm.) T. Moore = *E. minutum*

Elaphoglossum rhomboideum A. Vasco, Mickel & R. C. Moran

Elaphoglossum rhynchophyllum Christ = *E. lloense*

Elaphoglossum serpentinum A. Rojas & W. D. Rodríguez = *E. lloense*

Elaphoglossum squamipes (Hook.) T. Moore

Elaphoglossum subaequale T. Moore = *E. squamipes*

Elaphoglossum teleglottis Mickel = *E. lloense*

Elaphoglossum tripartitum (Hook. & Grev.) Mickel
Elaphoglossum wrightii (Mett. ex D. C. Eaton) T. Moore, see Excluded Species
Elaphoglossum xiphoides Mickel = *E. minutum*
Elaphoglossum sect. *Squamipedia* subsect. *Peltapteris* (Link) Mickel & Atehortúa = *Elaphoglossum* sect. *Squamipedia*
Microstaphyla bangii (Christ) Hieron. = *E. moorei*
Microstaphyla colombiana Maxon
Microstaphyla moorei (E. Britton) Underw. = *E. moorei*
Osmunda peltata Sw. = *E. peltatum* f. *peltatum*
Peltapteris Link = *Elaphoglossum* sect. *Squamipedia*
Peltapteris colombiana (Maxon) L. D. Gómez = *E. colombianum*
Peltapteris flabellata (Humb. & Bonpl. ex Willd.) C. V. Morton = *E. peltatum* f. *flabellatum*
Peltapteris flabellata f. *standleyi* (Maxon) C. V. Morton = *E. peltatum* f. *standleyi*
Peltapteris foeniculacea (Hook. & Grev.) L. D. Gómez = *E. peltatum* f. *flabellatum*
Peltapteris moorei (E. Britton) L. D. Gómez = *E. moorei*
Peltapteris peltata (Sw.) C. V. Morton = *E. peltatum* f. *peltatum*
Peltapteris peltata f. *flabellata* (Humb. & Bonpl. ex Willd.) L. D. Gómez = *E. peltatum* f. *flabellatum*
Peltapteris peltata f. *foeniculacea* (Hook. & Grev.) C. V. Morton = *E. peltatum* f. *flabellatum*
Peltapteris peltata f. *potentillifolia* (Christ) C. F. Reed = *E. peltatum* f. *flabellatum*
Peltapteris peruviana L. D. Gómez = *E. moorei*
Peltapteris tripartita (Hook. & Grev.) C. V. Morton = *E. tripartitum*
Rhipidopteris Schott ex Fée = *Elaphoglossum* sect. *Squamipedia*
Rhipidopteris flabellata (Humb. & Bonpl. ex Willd.) Fée = *E. peltatum* f. *flabellatum*
Rhipidopteris peltata (Sw.) Schott ex Fée = *E. peltatum* f. *peltatum*
Rhipidopteris rusbyi Christ = *E. moorei*
Rhipidopteris sphenophylla (Kunze) Fée = *E. peltatum* f. *flabellatum*
Rhipidopteris standleyi Maxon = *E. peltatum* f. *standleyi*
Rhipidopteris tripartita (Hook. & Grev.) Fée = *E. tripartitum*
Rhipidopteris tripartita var. *subbiternata* Hieron. = *E. tripartitum*

APPENDIX 3. List of exsiccatae reviewed. Collector names are organized alphabetically; collector numbers in boldface refer to types. The number in parentheses refers to the species (infraspecies) number assigned in this monograph. Only the first collector's name is given for accessions with multiple names.

Abbott 1853 (13b); **Aceby** 490, 566, 761 (10); **Acevedo-Rodríguez** 13844 (13b); **Aguilar** 4510 (15), 5382 (13b); **Albert de Escobar** 6000 (9); **Alfaro** 523 (13a), 610, 1161 (15), 4456, 5608 (13b); **Allard** 22122 (13b); **Allen** 15275, 15409, 503, 508 (13b), 1260 (13c), 1951 (10); **Almeda** 5807 (13b); **Alston** 161 (13b), 6472 (9), 6982 (13a), 7201 (15), 7660 (13b), 8187 (13a), 8212 (13b), 8235 (14), 8375 (9); **Anderson** 3271, 3300 (13b); **André 3114** (1), 186, 1185 (13b), 2557, 3381 (13a); **Angulo** 364 (13c); **Ankersen** 174 (13b); **Araquistain** 2611 (13b); **Arbeláez** 922 (9); **Argent** 94 (13b); **Arias** 0135 (9); **Asplund** 8709 (16), 19710 (13c); **Atehortúa** 1065, 1071 (9); **Atwood** 3913 (13b); **Axelrod** 3237 (13b); **Aymard** 2444 (13b).

Bach 1650, 1881 (9); **K. Baker** 13961 (13c); **M. A. Baker** 5771 (13c); **H. Balslev** 3143 (16), 3230, 4688, 4739 (13b), 60594 (10); **Bang 558** (11), 1791 (15); **Barclay** 5969 (1), 9451 (13b), 9453 (13c); **Barfod** 41358 (13b), 48608, 48763 (13a); **Barkley** 40047, 40355 (13b); **Barreto** 8851 (13b); **Barrington** 496 (9); **Bartholomew** 3326, 3327 (13b); **Beck** 1426 (9), 24667 (11); **Beitel** 85271 (13b); **Bell** 662 (16), 665 (9); **Berlin** 445 (13b); **Betancourt** 179 (13b); **Bittner** 104, 107, 148 (15), 2585 (9); **Blomquist** 12746 (13b); **Boeke** 1015 (13b); **Bøgh** 47860 (9); **Bohs** 1825 (13b); **Boom** 7460 (13a), 7497 (13b), 9195 (13a); **Bourgeau** 3158 (13b); **Boyle** 5975 (13b); **Brade** 97, 166 [HB no. 9813] (13b), 194 (13a), 5290, 6447, 15206 (15), 15379 (10), 15531, 16472, 20830, 21270 (15); **Brandbyge** 30577 (10), 42881 (15); **Breedlove** 21662 (13b), 22733 (15), 27432, 27432 (10); **Brenes** 4025 (13a), 14201 (13b), 15077 (13c), 15153 (13b), 16131 (13a), 16137, 21237 (13b), 22420 (13a); **E. G. Britton** 974, 2664 (13b); **N. L. Britton** 2161, 2480, 6187, 7593 (13b); **Brown** 17828 (13b); **Bryan** 526 (15); **Buchtien** 5297 (11); **Bües** A41, **1572** (11); **Burger** 5680, 5807 (13b), 7374 (15).

Callejas 5076, 9148 (13b); **Calzada** 8341, 8805 (13b); **Camp** E-810 (13b), E-2882 (15), E-3419 (7); **Campos** 1713 (13b); **Campos-Porto** 2645 (13b); **Carlson** 3360 (13b); **Carter** 5251 (13b); **Casal** 28a (13b); **Casañas** 233 (13a), 252 (13b); **Cayola** 2847 (11); **Cazalet** 5180 (13b), 5479 (15); **Cedillo** 3321 (13b); **Cerón** 6465 (13a), 17303 (13b); **Cházaro** 6791 (15); **Christenhusz** 4171 (8), 5400 (13b); **Chrysler** 1802, 4902 (13b); **H. Churchill** 4839 (13a), 4840, 5865 (13b); **S. P. Churchill** 16890, 18340, 18341 (13b); **Clark** 3634, 7513 (13a), 4505pp (16), 4505pp (13b), 7422 (16), 12471 (13b); **Clarke** 4963 (10); **Cleef** 7839 (1); **Clute** 83 (13b); **Cogollo** 2917 (13c); **Condack** 250, 318 (15); **Correa** 8044 (13c), 8213 (13b), 8577 (13c), 8578 (13b), 8586 (13a); Cotton A1546 (6); **Couthouy** 26 (16); **Croat** 39143 (13b), 40328 (10), 47349 (15), 54442 (9), 60433 (13c), 60591A, 63771, 64055 (13b), 68139, 68171 (13c), 70389 (13b), 73680 (7), 100818 (13c); **Cuatrecasas** 11911 (1), 12863, 12998 (13b); Curran 5 (13b).

Daly 13117 (13b); **Danin** 76234 (13b); **Davidse** 23878 (15), 24572 (10), 24575 (13b), 24914, 25269, 25834 (15), 35362, 35900, 35975, 36200, 36767, 37298 (13b); **Davidson** 746 (10); **de Avila** 728, 728 (13b); **deWolf** 353 (13b); **C. Díaz** 7565 (13b), 9669 (15); **S. Díaz** 1306 (13b); **Dodge** 4517, 16998 (13b); **Dodson** 7429, 7581 (13b), 10685 (15), 10770 (16), 10815 (9), 10928, 12016, 14166 (13b); **Dorr** 7301, 7402, 8249 (9); **Dressler** 86 (10), 154, 1604 (13b); **Dudley** 10490 (11); **Duke** 13225, 13847 (13b); **Duque** 162 (1); **A. Duss** 4135 (8); **P. Duss** 1617, 4147 (13b); **Dwyer** 492 (13b), 8708 (10).

Eberhardt 100, 348, 593 (9), 598 (13a); **Echeverri** 152 (9); **Ekman** 4618, 5337, 6757, 8858, 11835, 14375 (13b), 14764 (10); **Endara** 259 (16); **Engel 118** (9); Engelmann RE231 (15); **Eriksen** 59211 (15), 91224, 91224 (9); **Espinoza** 53 (13b); **Esseichick** 117, 118 (13b); **Estrada** 1850 (13a); **Evans** 90 (15).

Fagerlind 713 (13b), 1255 (13c); **Fay** 1455 (13b), 3164, 3177, 3232, 3344 (16), 3604 (13c); **Fendler** 263 (13c), 286 (9), 361, 278 (13b); **Fernándes-Alonso** 24771 (13b); **A. Fernández** 1433 (15); **E. Fernández** 2078, 2078 (9), 2419 (11), 2537, 2626 (9), 3110 (11), 3484, 3498 (9); **A. Fernández-Pérez** 5352, 5439, 5491 (13b); **Figueroa** 70 (13b); **Filskov** 37096 (16); **Fink** 109 (13b); **Fisher** 98 (13b); **Folsom** 6677 (13a); **Fonnegra** 1966 (13b); **Forero** 2709, 5067 (13b); **Foster** 7763 (11), **10891** (12), 10894 (13a), **11978** (10); **Franco** 1183 (13b), 1259, 1869, 2159 (13a), 2883 (9); **Freire** 3011 (15); **Fryxell** 2553 (13b); **Fuentes** 8829, 11706 (11); **Fuertes** 516, 1088 (13b).

Galeano 3703 (13b); **Gamboa** 995, 1159, 1302 (15); **Gastony** 240, 624 (13b); **Gavilanes** 848 (1); **Gentry** 24416 (13b), 26546 (13a); **Ghiesbreght** 397 (13b); **Giraldo-Cañas** 379 (13b); **Gittins** 4155, 4226 (13b); **Glassman** 2109 (13b); **Glaziou 3550** (15); **A. Gómez** 685 (5); **L. D. Gómez** 21843 (15); **Gómez-Dominguez** 1019 (13b); **F. González** 3116 (14); **M. F. González** 579 (13b); **M. L. Grant** 9809 (13b), 9815 (13a), 10210 (9); **V. Grant** 863 (13b); **Grayum** 4993 (13c), 7101 (13b), 7431 (15); **Grijalva** 595, 1211 (13b); **Grubb** 1293 (13b), 1309 (9), 1320 (13a), 1340 (9).

Haber 2870, 5193 (13b), 8536, 9563 (13a); **Hagemann** 660 (9), 1359 (1), 1543 (13b), 1846, 1997 (9); **Hahn** 701 (13b); **Hallberg** 1436, 1514, 1726 (13b); **Hamilton** 4122 (13c); **Hammel** 7477 (13b), 17461 (13a); **Harling 18092**, 22455 (3), 22685 (16); **Harris** 7490, 10125 (13b); **Hartley** 13337 (13b); **Hatch** 88 (13b); **Haught** 4494, 4638 (13b), 5234 (13a); **Hauke** 217, 476 (13b), 477 (13c); **Hawkins** 529 (13b); **Hazlett** 8017 (13b); **Heinrichs** 826 (15); **Henipam** 6719 (13b), 6878 (13a); **Henrich** 206, 411 (13b); **Herrera** 1026, 3176 (13b); **Hess** 218, 2802 (13b); **Heyde** 3216 (13b); **Hill** 13, 17848 (13b); **Hinton** 10756, 14273 (13b); **Hodge** 22 (8), 1784 (13b), 2297, 2790 (8), 2803 (13b), 6630 (9), 6986 (13b); **Holdridge** 771, 799, 799, 1592 (13b); **Holm** 191 (13b); **Holm-Nielsen** 425, 532 (13c), 1365 (7), 2915, 2944, 3035, 4099a (13b), 5657 (9), **6168** (14), 7083, 18151, 18422, 24796 (16), 41810 (1); **Holst** 3894, 5517, 5700 (13b); **Hoover** 1611, 1614 (13a), 2897 (9); **Horich** 428 (15); **House** 1129 (15); **Howard** 8542, 12289, 16016 (13b); **Huertas** 5928 (1); **Hunnewell** 14609 (15); **Hutchison** 4753, 5825 (15).

Idrobo 979, 1102, 1490 (13b), 2992 (1); **Iltis** 483, 2229a (13b).

James 1973316 (13b); **Jameson** 2 (13b), 32 (13a), 44 (16), 108, 137 (13b), 207 (16), 451 (9); **Janovec** 1419, 1421 (13b); **J. Jaramillo** 7960 (16); **N. Jaramillo** 678 (13b); **Jaramillo-M** 3072, 3678 (15), 3773 (9), 3874 (13b), 5171 (1), 5355 (15), 5919, 5973 (1), 6381 (15), 7194 (13b), 7430, 7432, 7561 (9); **A. Jiménez** 401 (13b); **I. Jimenez** 2289 (10), 701 (11), 1242, 2151 (9), 2191, 2274 (12), 2888 (15); **Jones** 1020, 3268 (13b); **Jordán** 338, 373 (9).

Kerr-Valentic 73 (9); **Kessler** 6561, 6664 (9), 6742 (15), 6961 (11), 7078 (11-hybrid?), 7280, 7389, 7536 (9), 7689, 7689, 7948 (12), 8300 (10), 9137, 9418, 9502, 9548 (9), 10944 (10), 11319 (9), 11690 (12), 11808, 11846, 12057 (9), 12171 (11), 12172, 12947 (9); **Killip** 9012 (13a), **11365** (5), 11618 (13b), 11619 (13a), 17748 (15), 17867 (1), 20095 (13b), 22781, 23206 (13a), 26016, 33161, 38909 (13b); **King** 7695 (11); **Kirkbride Jr.** 1925, 2127 (13a), 2136 (13b); **Knight** 686, 1155 (13b); **Köster** 871 (10); **Krömer** 2838 (13b), 2873 (10); **Kunkel** 632 (13a).

Labiak 1253 (15), 2855 (9); **Laegaard** 51596B, 51616, 51668 (13b), 54626 (16); **LaFrankie** 1024 (13b); **Larsen** 35385 (13b); **Lehmann** 1041 (13a), 3641 (14), 4928 (1), 6949 (15), 7405 (9), 7658 (6); **Lehnert** 384 (11-hybrid?), 1253 (13b), 1254 (13a), 1316 (12), 1409 (6), 1424 (9), 1460, 1463 (1), 1491 (9), 2259 (15), 2309 (9); **Lellinger** 96, 547 (13b), 633 (8), 1961 (15); **Lems** 650203 (13b), 64012702-6 (13a); **Lent** 30, 702 (13b), 717 (15), 3699 (13c); **León** 10401, 12034 (13b); **Leonard** 14555 (13b); **Lesica** 4157 (13b); **Lewis** 293 (13b); **Liebmann** 86 (13b), 2427 (10); **Liesner** 9924, 16908, 17717 (13b), 21548 (13a), 21661, 25064, 25076, 25385, 26619, 26629 (13b); **Lindig** 270 (13c); **Liogier** 19916, 21650 (13b); **Little** 9377 (9); **Lloyd** 150 (8), 348 (13b), 890 (8), 925, 4209 (13b), 4276 (15); **Løjtnant** 12069 (1), 14038 (16); **Lorea** 1920, 3168 (13b); **Lozano** 3489 (2), 4684 (1); **Luer** 8682 (9); **Lugo** 1791 (13b); **Luteyn** 6117 (15), 8245 (9), 10693, 10745 (13b), 10765 (13a), **11002** (2), 12248 (5), **14682** (4).

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APPENDIX 4. Distribution by country (or island) for the taxa of *Elaphoglossum* sect. *Squamipedia*. Endemic species are in boldface. The number of taxa per locality appears in parentheses.

Belize (1): *E. peltatum* f. *peltatum*

Bolivia (6): *E. lloense*, *E. minutum*, *E. moorei*, *E. nidiforme*, *E. peltatum* f. *flabellatum*, *E. squamipes*

Brazil (3): *E. minutum*, *E. peltatum* f. *peltatum*, *E. squamipes*

Colombia (10): *E. andreanum*, *E. anthracinum*, ***E. colombianum***, *E. lloense*, *E. minutum*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. rhomboideum*, *E. squamipes*

Costa Rica (6): *E. lloense*, *E. minutum*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. squamipes*

Cuba (2): *E. peltatum* f. *peltatum*, *E. minutum*

Dominica (2): *E. feei*, *E. peltatum* f. *peltatum*

Dominican Republic (2): *E. minutum*, *E. peltatum* f. *peltatum*

Ecuador (15): *E. andreanum*, *E. anthracinum*, ***E. blepharis***, ***E. bryogenes***, *E. concinnum*, *E. deltoideum*, *E. lloense*, *E. minutum*, *E. nidiforme*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. rhomboideum*, *E. squamipes*, ***E. tripartitum***

El Salvador (2): *E. peltatum* f. *peltatum*, *E. squamipes*

Guadeloupe (2): *E. feei*, *E. peltatum* f. *peltatum*

Guatemala (3): *E. minutum*, *E. peltatum* f. *peltatum*, *E. squamipes*

Guyana (3): *E. minutum*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*

Haiti (1): *E. peltatum* f. *peltatum*

Honduras (2): *E. minutum*, *E. peltatum* f. *peltatum*

Jamaica (2): *E. minutum*, *E. peltatum* f. *peltatum*

Martinique (1): *E. peltatum* f. *peltatum*

Mexico (3): *E. minutum*, *E. peltatum* f. *peltatum*, *E. squamipes*

Nicaragua (1): *E. peltatum* f. *peltatum*

Panama (6): *E. lloense*, *E. minutum*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. squamipes*

Peru (9): *E. concinnum*, *E. lloense*, *E. minutum*, *E. moorei*, *E. nidiforme*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. squamipes*

Puerto Rico (1): *E. peltatum* f. *peltatum*

Venezuela (6): *E. lloense*, *E. minutum*, *E. peltatum* f. *flabellatum*, *E. peltatum* f. *peltatum*, *E. peltatum* f. *standleyi*, *E. squamipes*

Erratum

Liede-Schumann, S. & U. Meve. 2013. The Orthosiinae Revisited (Apocynaceae, Asclepiadoideae, Asclepiadeae). Ann. Missouri Bot. Gard. 99: 44–81.

Liede-Schumann and Meve inadvertently left out the basionym reference for *Scyphostelma veleziae*. Here is the corrected combination.

24. Scyphostelma veleziae (Morillo) Liede & Meve, comb. nov. Basionym: *Cynanchum veleziae* Morillo, Ernstia 2(1–2): 10. 1992. TYPE: Colombia. Depto. del Quindio, Mun. de Genova, camino a finca Servia–Valle Chiquito en borde del bosque ante de llegar al subpáramo, 3000 m, 16 July 1990, *M. C. Vélez, C. A. Agudelo, L. F. Hoyos, V. M. Agudelo & N. J. Ocampo 2027* (holotype, HUQ not seen; isotypes, COL!, VEN!).

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Cover illustration. ***Siculosciadium nebrodense*** **(Guss.) C. Brullo, Brullo, S. R. Downie & Giusso, drawn by Salvatore Brullo.**

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EVODEVO AND THE PROMISE OF UNDERSTANDING MORPHOLOGICAL TRANSITIONS IN EVOLUTION[1]

Lisa M. Nagy[2] *and Terri A. Williams*[3]

ABSTRACT

The field of Evolutionary Developmental biology arose with the promise of new approaches to answering longstanding questions of comparative biology. Here we review the fruits of that promise some decades later. We chose three areas of arthropod EvoDevo—evolution of body plans, segment number, and appendage morphology—to provide an overview for the nonspecialist of how these issues have been clarified by the comparative analysis of regulatory gene networks. In all cases, we identify substantial progress and novel insights provided by the tools and perspective of EvoDevo. We also recognize that some core questions remain unanswered, and we reflect on how discoveries in EvoDevo fit in the landscape of other progress in phylogenetics, population biology, and genomics, facilitated by a new and ever-expanding set of molecular tools for comparative studies in evolution.

Key words: Appendage development, arthropods, development, evolution, segmentation.

What meets the eye when we cursorily inspect nature is an overwhelming variety of morphological forms. One current strategy in biology to explain how diverse forms might have evolved is to compare the regulation of body patterning during development. If we can grasp how form develops among a number of related species, we can hypothesize how modifications in development create distinct morphological forms over evolutionary time. The contemporary study of how developmental patterning evolves—EvoDevo—relies primarily on understanding the gene regulatory pathways that modulate development. At the same time, EvoDevo draws on longstanding intellectual enterprises in science. Here, we briefly describe the development of EvoDevo as a modern field. Then, using three specific examples related to our research in arthropods, we evaluate the success of this approach.

One of the oldest insights into animal diversity is that variety can be partitioned and comprehended by grouping similar animals together. Discriminating similarities and differences among animals and using those to erect categories of distinct types of animals goes back at least to Aristotle and was a continuing thread in the natural sciences as they developed over the next two millennia. By the late 18th to early 19th

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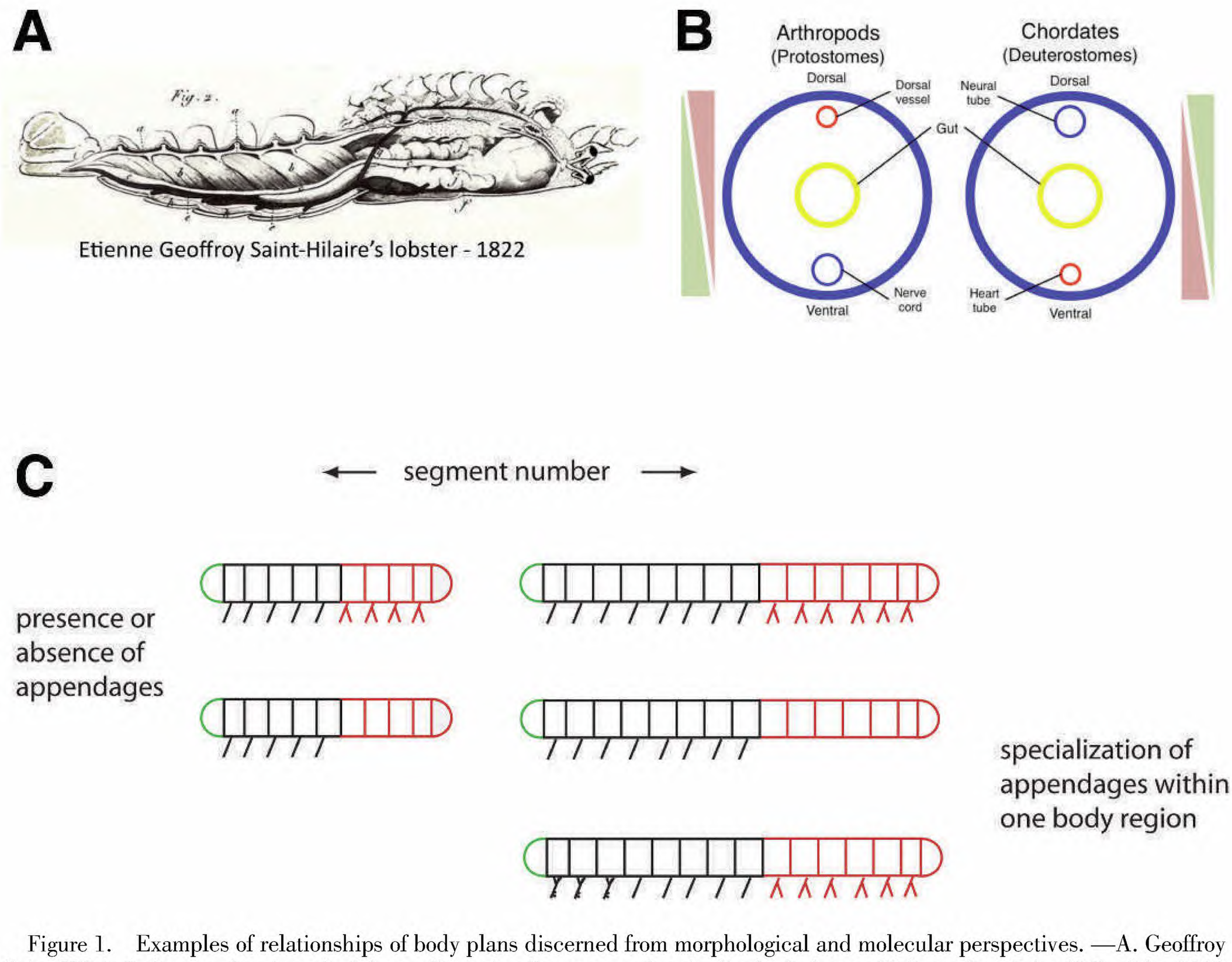


Figure 1. Examples of relationships of body plans discerned from morphological and molecular perspectives. —A. Geoffroy Saint-Hilaire's famous drawing of a lobster dissection "une coupe longitudinale du homard" from plate 7 (p. 119) of the 1822 article "Considérations générales sur la vertèbre." In our Figure 1, the lobster is shown lying on its back, with its ventral nerve cord above the internal organs. In the inverted orientation herein, the body plan of the arthropod resembles that of the vertebrate. —B. Diagrammatic views of the protostome and chordate body plans. The dorsoventral structures occupy opposite sides of the body and are patterned by inverted domains of the diffusible growth factors (green gradient: *dpp*/BMPs) and their inhibitors (red gradient: *sog*/Chordin; from DV-axis-inversion, L'ontogenese, Wikipedia). —C. Generalized pattern of arthropod tagmatization. The diagram shows a simplified representation of the patterns of segmental diversification within arthropods: changes in segment number, presence or absence of segments on a particular segment, and specialization of appendages within one body region.

century, the conceptual framework that developed for this enterprise used the idea of homology (a structure similar under any transformation) versus analogy (any structure of similar function) to interpret parts of animals, and the similarities among animals were generalized using the conceptual model of an archetype (see Russell, 1917; Hall, 1994, 1999). The use of archetypes was a powerful tool for making comparisons highly explicit between taxa since the archetype was essentially a series of hypotheses about the morphology of a particular taxon. This theoretical framework, informed by a sophisticated grasp of the body plans of distinct taxa, led to specific discoveries (e.g., Goethe's discovery of the human intermaxillary bone) as well as broad sweeping theories (e.g., Geoffroy Saint-Hilaire's theory that vertebrates are essentially arthropods flipped onto their backs, or Richard Owen's demonstration via his vertebrate archetype that vertebrates are built from repeated parts (Fig. 1A; Russell, 1917; Appel, 1987; Hall, 1999).

The theoretical framework of comparative morphology underwent a radical transformation at the end of the 19th and early 20th century due to two developments: Darwin's theory of evolution by natural selection and the modern synthesis of Mendelian genetics and population genetics (see Mayr, 1993; Gilbert et al., 1996; Bowler, 2003). The growth and predominance of these ideas had the effect of diverting the understanding of morphology from comparisons of form to a search for genetic (or other reductive) causes of form. In this new light, many of the hypotheses of the previous century disappeared. The conundrums of the past century were not resolved; they simply became unimportant in the new way of conceiving of natural phenomena. However, while old theories and hypotheses based on archetypes were not part of the modern research

agenda, they were still embedded in most textbooks dealing with animal diversity. For example, textbooks still presented generalized schemata to illustrate different phyla (see Brusca & Brusca, 2003) with traits of those schemata clearly defined (so-called true segmentation vs. pseudosegmentation vs. no segmentation). The persistence of these schemata was important to the emergence of EvoDevo as a field because they provided the background for comprehension of the importance of different fundamental body plans to metazoan diversity.

Developmental genetics made rapid progress in understanding the genetic regulatory control of external morphology in a few select model organisms. EvoDevo as a field gained momentum with the discovery that many of the genetic regulatory mechanisms that drive patterning in model organisms were broadly shared. A commonly cited example is *Pax*6, a gene for a transcription factor used to position the eyes in diverse organisms, even eyes that are not homologous (reviewed in Gehring, 2002). Carroll et al. (2001) postulated that a finite genetic toolkit existed for patterning embryos, and following on earlier ideas that changes in gene regulation were critical for phenotypic diversity (Jacob, 1977), popularized the idea that tinkering with this conserved set of regulatory genes could produce diverse body plans. This hypothesis reanimated some of the old questions about how the basic body plans of animals relate to one another. For example, a regulatory loop that patterned the dorsal axis of arthropods, but the ventral axis in vertebrates, resurrected Geoffroy's theory of vertebrates being upside-down arthropods (Fig. 1B; De Robertis & Sasai, 1996). From a gene's eye view, the genetic basis underlying morphological variation appeared to be remarkably similar throughout metazoans (see Carroll, 2005). This led to an initial enthusiasm that a modern, gene-based EvoDevo would resolve old issues of comparative morphology and ultimately be able to explain the great morphological radiations.

Here, we provide a brief review of progress on EvoDevo as viewed through the lens of examples relevant to our research dealing with the diversification of arthropods. In arthropods, a segmented body plan covered by a chitinous exoskeleton has produced evolutionary radiations of highly diverse and elaborated external morphologies. Many body segments bear appendages, and these are often specialized to perform distinct functions, both along the body axis in any particular species as well as between species. Much of arthropod diversity can be ascribed to segments and their appendages. In the vignettes that follow, we reflect on the power of the EvoDevo approach to shed light on that diversity, and we conclude with reflections on why some questions have proved more tractable than others and what future approaches might include. We examine three features of variation of the arthropod body plan: (1) tagmatization and limb character along the anterior-posterior (A-P) body axis, (2) segment number, and (3) limb morphology. In each case, we outline the variation to be explained, the hypotheses generated from the genetic model system, the existing data, and what they explain.

Tagmatization

Variation to be Explained

Arthropod diversity can be grossly characterized by variation in the numbers and specializations of segments. Most taxa have a fixed total number of segments, but some branchiopod crustaceans and some centipedes have a varying total number of segments. A feature common to all taxa is tagmatization, the regionalization of the body into distinct blocks of segments, namely, the head, thorax, and abdomen (Fig. 1C). Not only does total segment number vary between species, but also the number of segments in any particular body region can vary among taxa, e.g., the insect thorax has three segments, the decapod crustacean thorax has eight. Furthermore, overlaid on this divergence in tagma between distantly related taxa are modifications to tagma among even closely related taxa. For example, among decapods with eight thoracic segments (e.g., crabs, shrimp, lobsters) some might have all eight specialized for locomotion while others divide the eight into functional subspecialties. A common example is the appendages on the anterior thoracic segments that are modified to function with the head segments in feeding.

In general, the variation in arthropod segmentation can be grouped into three categories: (1) whether the total number of body segments is variable or fixed; (2) if it is fixed, how one taxon differs from another in total segment number and tagmatization; and (3) how body regions within a taxon are modified. These types of variation yield diverse patterns of segmentation among arthropods, patterns that have long been studied by naturalists (see Bateson, 1894; Lankester, 1904). Indeed, standard patterns of segmentation were so well known that in 1894 Bateson could catalogue instances of exceptions found in nature. These exceptions included a kind of variation in which one segment in a series assumed the character of another segment; Bateson called this phenomenon "homeosis." The recognition many years later that

homeosis could be caused by mutations of a single gene (Bridges & Morgan, 1923; Lewis, 1978) became a springboard for thinking about how patterns of segmentation might have evolved (Goldschmidt, 1940; King & Wilson, 1975; Lewis, 1978).

HYPOTHESES FROM DEVELOPMENTAL GENETICS

The discovery of the genetic basis of homeosis in flies by Lewis (1978) laid the foundation for understanding not only the developmental genetics behind segmental patterning in the dipteran *Drosophila melanogaster* Meigen, but also the evolutionary diversification of segment character. Using genetic analysis, the genes in the *Antennapedia* and *Bithorax* complexes of *D. melanogaster* were shown to control the development of the fruit fly body, with the exception of the termini (Lewis, 1978; Kaufman et al., 1980). The *Hox* genes have the unusual feature that their order along the chromosome mirrors their domains of function along the A-P body axis. This chromosomal linearity also suggests deep ancestral origins from multiple gene duplication events (Lewis, 1978).

Lewis discovered that the three posterior *Hox* genes in *Drosophila melanogaster* define the limbless abdominal body region. Given that the limbless abdomen is a defining feature of hexapods, Lewis (1978) speculated that the abdominal *Hox* genes originated at the base of the insect lineage through a serial gene duplication process. Arthropods with legs on all their trunk segments were predicted to lack these genes in their genomes, thereby avoiding the repression of limb development in the posterior region of their bodies. However, nearly all arthropods, as well as their closest relatives, the *Onychophora* Grube, or velvet worm phyllum, have a full complement of *Hox* genes, and the simple hypothesis correlating new *Hox* genes with arthropod diversification was abandoned (Grenier et al., 1997; see below for discussion of why loss and gain of *Hox* genes as a plausible genetic change underlying arthropod diversification may yet be revived on a smaller scale). The next hypotheses correlating the evolution of tagma with *Hox* control of segment identity were built with the knowledge that nearly all arthropods have a full complement of *Hox* genes.

Once cloned, the *Hox* genes were identified as a family of transcription factors (McGinnis et al., 1984; Scott & Weiner, 1984) now recognized as a shared feature of multicellular animals. *Hox* genes are found throughout the Metazoa and are frequently clustered in the genome (reviewed in Lemons & McGinnis, 2006). Interestingly, less than 5% of the *Bithorax* locus identified by Lewis is devoted to the coding sequence of the transcription factors. (Bender et al., 1983). These *cis*- regulatory regions scattered throughout the remainder of the locus contain binding sites for proteins that regulate the precise spatial and temporal expression of *Hox* genes. *Hox* genes function, in many animals, to pattern region-specific cell fates along the body axis. They realize this function by establishing specific expression domains along the body axis and regulating large suites of downstream target genes within these domains. Precisely how this results in the ultimate body plan of the animal is not completely known for any animal, although it is best understood in *Drosophila melanogaster*. Given the understanding of the *Hox* gene function in *D. melanogaster*, it was hypothesized that arthropod segmental diversity would correlate with changes in the regulation, both upstream and downstream of the *Hox* genes (Grenier et al., 1997). Evidence for intraspecific regulatory changes in *Hox* gene expression domains and in *Hox* gene targets followed in short order (for summary of regulatory changes in *Ubx*, see Barton et al., 2007). Below, we briefly recount some of the current data that support a model of how shifting *Hox* boundaries and *Hox* targets might explain how tagma evolved within crustaceans.

EXISTING COMPARATIVE DATA

Crustaceans use the last three of their five head appendages for feeding. However, in a number of taxa, appendages on anterior thoracic segments have been recruited to also function in feeding. For example, decapods have eight thoracic segments but only five pairs of locomotory limbs; the three anterior thoracic segments are modified for feeding. The first indication that the boundary between feeding and nonfeeding thoracic limbs might be under *Hox* control came from examining the expression of *Ubx* protein in crustaceans with various numbers of thoracic feeding limbs (Averof & Patel, 1997). Subsequent expression studies in isopod and branchiopod crustaceans supported this hypothesis (Abzhanov & Kaufman, 1999, 2000; Shiga et al., 2002). More recently, it was demonstrated that RNA interference (RNAi) silencing of *Ubx* in the peracarid crustacean, *Parhyale hawaiensis* Dana, produces a decrease in the gene expression of *Ubx* relative to wildtype in the second and third thoracic segment. This decrease in expression causes a transformation of those limbs toward the feeding morphology of the first thoracic appendage (Liubicich et al., 2009). Conversely, ectopic expression of *Ubx* produces a transformation of feeding appendages toward more posterior limb morphologies (Pavopoulos et al., 2009). These functional results are consistent with

a model in which graded levels of *Ubx* protein control the character of limbs along the thorax: high levels of *Ubx* protein in the posterior thoracic limbs specify thoracic identity, whereas lower levels in anterior limbs specify a less elaborated, thoracic morphology. These are compelling results and provide a plausible model for re-specification and specialization of anterior thoracic appendages during crustacean evolution.

The paradigm of shifting boundaries is, however, only useful for a subset of the morphological transitions observed within the arthropods. Another body of evidence is accruing that suggests changes downstream of the *Hox* genes will play critical roles in other morphological transitions. For example, in flies, two *Hox* genes, *Ubx* and *abdA*, suppress limb development in the abdomen by direct repression of limb development genes (Vachon et al., 1992). The crustacean *Artemia* Leach (brine shrimp) expresses *Ubx/abdA* protein throughout the limb-bearing segments, but in *Artemia*, these genes do not appear to repress limb development. Interestingly, the *Artemia Ubx* gene is a weak repressor of the limb pathway, and differences in the translational product or amino acid sequence between *Artemia* and *Drosophila* correlate well with their respective strength of repression (Galant & Carroll, 2002; Ronshaugen et al., 2002; Shiga et al., 2002). In addition, it appears that the *Artemia abdA* mRNA is not translated into protein (Hsia et al., 2010). Thus, while progressively posterior boundaries of the *Bithorax* complex genes are maintained in this crustacean, they do not share the same regulatory targets as insects and do not regulate boundaries in limb morphology. In sum, *Hox* genes show a remarkable degree of conservation throughout the evolution of the Metazoa; at the same time, evolutionary changes in where they are expressed and in their specific functions can help explain evolutionary transitions in arthropod tagma.

WHAT IT DOES AND DOES NOT EXPLAIN

Of the patterns of segmental variability to be explained in arthropods, the *Hox*-based model addresses one pattern very well: how segments within a tagma are modified in a graded manner. The model does not address changes in segment number in any particular body region, i.e., how a taxon might evolve from having a thorax with 12 to eight segments. This is in part because the model focuses on limb morphology, yet tagma are not defined just by limb morphology but also by other segmental structures. The comparative analysis of *Hox* genes has also yielded the unexpected finding that in some species *Hox* genes do not pattern nonterminal regions of the arthropod body plan. For example, while the posterior segments of the branchiopod crustacean, *Artemia*, do not bear limbs, no *Hox* gene expression has been detected in this region (Averof & Akam, 1995). Secondly, although the vast majority of morphological change occurs at boundaries between body tagma, in some cases taxa differ mid-tagma, e.g., the collembolan furca, which appears in the middle of the abdomen, from the fourth abdominal segment. (The furca is a fused, forked appendage that gives the name of springtails to collembolan insects.) This region is not at an expected boundary of the *Hox* genes and has not (as yet) been shown to be associated with any novel boundaries of *Hox* genes. This is related to another, much more common phenomena not encompassed by this model. Numerous crustaceans have larval stages with patterns of appendages quite distinct from their adult stages. Specifically, they show differences in segmentation patterns at sequential stages of the lifecycle that do not consist of graded changes at boundaries. Candidates for the genetic control of these morphological transitions are not yet obvious.

SEGMENT NUMBER

VARIATION TO BE EXPLAINED

Segment number varies among the greater than million species of arthropods, ranging from hundreds in some millipedes (Enghoff et al., 1993) to eight in ostracod crustaceans (Schram, 1986). Interestingly, most classes and orders of arthropods do not vary in segment number (with a few noteworthy exceptions, e.g., the geophilomorph centipedes; Minelli & Bortoletto, 1988), and segment number is a defining character for some major lineages. Unfortunately, the paradigm of using *Drosophila melanogaster* as a starting point for hypotheses about the genetic/developmental control of a morphological character is not possible with the case of segment number. Insects do not vary, for the most part, in total segment number, and dipteran insects form their segments in a highly derived manner. Mutations that increase segment number have not been identified in *D. melanogaster*. However, vertebrates show lineage-specific diversity in segment number and share with arthropods the ancestral mode of adding segments sequentially during development. Therefore, we use models of segment development from vertebrates to consider variation in segment number among arthropods. This comparison is supported not only by the shared fact of sequential segment addition but also by the finding that a number of the regulatory genes that

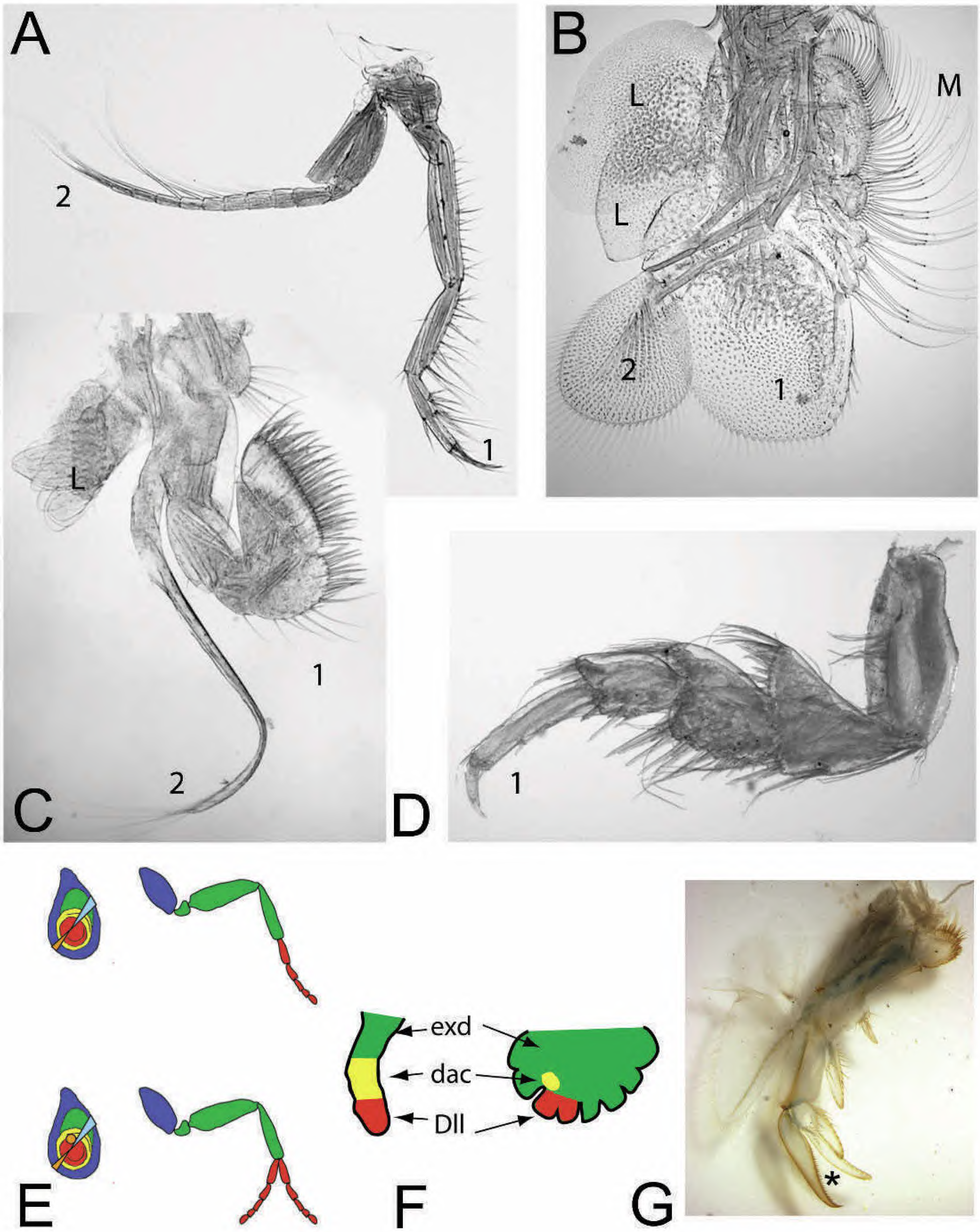


Figure 2. A–D. Variety in arthropod limb morphology, using crustacean examples. —A. Thoracic limb of the mysid shrimp, *Americamysis bahia* Molenock. —B. Thoracic limb of the fairy shrimp, *Thamnocephalus platyurus* Packard. —C. Anterior thoracic limb (maxilliped) of the grass shrimp, *Paleomonetes pugio* Holthuis. —D. Thoracic limb of the isopod, *Cirolina concharum* Lat. The two main branches are labeled 1 and 2, with additional lobes labeled as medial (M) or lateral (L). Note that beyond the fundamental variability in number of branches and lobes, limb parts are highly variable in terms of shape, proportion, and setal numbers and morphology. —E. Patterning in the leg disc of *Drosophila*. Diagram at top indicates signaling along the A-P segment boundary, which initiates PD outgrowth of the leg. The genes that establish the PD axis—*Distal-less* (red), *dachshund* (green), and *extradenticle/homothorax* (blue)—are activated in circular domains in the larval leg disc by a combination of signals (gold, light blue). As the larval leg disc grows and extends into the adult leg, these genes function to pattern three domains along the PD axis of the leg (diagram at bottom). Experimentally initiating new PD outgrowths by misexpression of a signal (gold) gives rise to artificially branched legs. F, G. Comparative expression data in limbs of varying

operate in vertebrate segmentation play similar roles in arthropods (Peel et al., 2005).

HYPOTHESES FROM DEVELOPMENTAL GENETICS

In vertebrates, segments arise from embryonic somites, which develop sequentially in a head-to-tail direction in the embryo (Fig. 1D). Somites bud off from the anterior presomitic mesoderm, an unpatterned region of active growth in the posterior of the embryo. Somites form at a species-specific rate, e.g., 30 min./segment in zebrafish, 90 min./segment in chickens, and 120 min./segment in mice (Romanoff, 1960; Tam, 1981; Schröter et al., 2008). At the same time, cells are added to the posterior of the presomitic mesoderm through the process of gastrulation, thereby allowing for continued development of segments. The size and number of somites depend on a dynamic interaction between three factors: the size of the presomitic mesoderm, the position of a posteriorly moving wavefront of determination, and oscillations of certain genes known as the segmentation clock (Fig. 1E). In general, in those vertebrate species examined, all use a similar molecular toolkit to run the segmentation clock: mainly genes of the *Notch*, *FGF*, and *Wnt* signaling pathways. In mice and fish, mutations in the oscillator genes cause severe defects in the somites. These pathways function to make pulses of signaling molecules in the presomitic mesoderm (Cooke & Zeeman, 1976; Elsdale et al., 1976; Palmeirim et al., 1997; Dubrulle et al., 2001; Sawada et al., 2001). Each cycle of the oscillator converts oscillations in time to a periodic pattern in space and results in the appearance of a pair of segments.

Gomez et al. (2008) asked whether the evolutionary variation in segment number between snakes, mice, chicken, and zebrafish could have resulted from developmentally varying either the size of the presomitic mesoderm, the position of the determination wavefront, or the periodicity of the segmentation clock. They found that in snakes, which have a high number of segments, the rate of oscillation of the segmentation clock was high relative to the growth and elongation of the presomitic mesoderm. Thus, snake embryos segment the presomitic mesoderm faster than other vertebrates, making smaller and more numerous somites. Do arthropods similarly control the size of segments generated per cell generation in the region of the embryo that forms segments to control segment number? As we point out below, understanding of the fundamental cellular processes of segmentation in arthropods lags behind that of vertebrates. Consequently, understanding the genetic control of segment number in arthropods is only just emerging.

EXISTING COMPARATIVE DATA

In most arthropods, segments form in an A-P progression (Sander, 1976; Minelli & Fusco, 2004; Peel et al., 2005). However, there are surprisingly few data that indicate whether segments form with a species-specific periodicity since patterns of segment addition are typically described only with reference to morphological stage and not developmental time. The assumption is that segment addition is regular and, in examining some crustaceans, we have found that segments are added with linear periodicity (Williams et al., 2012). Whether a regular periodicity in segment addition is widespread in arthropods remains unknown.

The combination of three features that control sequential segment addition in vertebrates—a growth zone, a determination wavefront, and a segmentation clock—has not been demonstrated for any arthropod. In general, most sequentially segmenting arthropods have a region of unpatterned tissue in the posterior that generates segments, i.e., a growth zone. However, the extent of the unpatterned tissue and its rate of growth or depletion during the process of segment addition are completely unknown. There is no evidence as of yet for a determination front in arthropods, at least of the kind found in vertebrates that is regulated by antagonistic gradients of signaling molecules. However, a growing body of literature suggests that the molecular toolkit that runs the vertebrate segmentation clock is conserved in spiders, sequentially segmenting insects, and recently, we have found evidence for the function of clock orthologs in crustaceans (Williams et al., 2012). In each of these cases, *Notch* signaling has been demonstrated to play a role in the proper formation of sequentially added segments.

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morphologies. —F. Simplified schematic of gene expression in limbs of two crustaceans. The genes that establish the PD axis include *Distal-less* (red), *dachshund* (yellow), and *extradenticle/homothorax* (green) and are expressed in a pattern similar to *Drosophila* (at left) and *Porcellio scaber* Latreille (at right). —G. In *Triops longicaudatus* LeConte, the three genes are expressed even in the unusually shaped limb bud of this species that develops into a highly modified (phyllopodous) limb form. The asterisk marks the two distal branches in the schematic of the limb bud and the adult limb.

WHAT IT DOES AND DOES NOT EXPLAIN

The discovery that *Notch* signaling plays a role in sequentially segmenting arthropods was initially hailed to indicate that vertebrate and arthropod segmentation was homologous. Closer comparison shows that, even among arthropods, disruption of the *Notch* signaling network has variable effects. In some species like *Drosophila melanogaster*, mutations in *Notch* signaling have no consequences for segmentation. While the discovery of a role for *Notch* signaling in arthropod segmentation is significant, a robust model of *Notch* function as well as the possibility that *Notch* signaling serves as a molecular oscillator remains unresolved. Thus, whether the segment number is regulated in arthropods via a balance between clock rate and rate of growth in the posterior awaits further research.

Limb Morphology

VARIATION TO BE EXPLAINED

The array of limb structures in arthropods is truly astounding (Fig. 2A–D; Brusca & Brusca, 2003). Even apparently simple, cylindrical limbs, like the walking legs of a crab, may have elaborate lateral outgrowths (in this case, functioning as gills and hidden beneath the carapace). Beyond cylindrical walking legs, arthropod limbs show adaptations for swimming, grasping, sensing, food handling, and many other functions. Correspondingly, limbs may be flattened into paddles, calcified for crushing pincers, or adorned with elaborate setal arrays. It is tempting to organize all arthropod limbs as variations on a theme of a single limb axis with medial or lateral outgrowths. However, it is not clear that this characterization is evolutionarily accurate, since some would argue that the ancestral limb had two fundamental branches (Walossek, 1993, 1999; Boxshall, 2004). In one major arthropod group, in extant Crustacea, the limb has two branches, i.e., the main axis is bifurcated. Thus, to understand some of the variation in limb morphology, there are at least three main questions to be addressed: (1) what patterns the main axial outgrowth; (2) how is the main limb axis bifurcated; and (3) what patterns the vast array of medial and lateral outgrowths that occur proximally on the limb axis? In addition to these main categories of variation, there are numerous features of appendages that differ widely between limbs, both within and between taxa, e.g., setal type and number, cuticular thickness and specialization or jointing, etc. This variation is often crucial to functional differences between limbs and also needs to be explained.

HYPOTHESES FROM DEVELOPMENTAL GENETICS

In *Drosophila melanogaster*, limb primordia are positioned at the boundary that defines the posterior portion or compartment of each segment. Subsequently, via signaling activated at the A-P compartment boundary, limb axes are defined and proximodistal (PD) elongation occurs. The gene network involved in patterning the PD leg axis is well described (Fig. 2E–G; reviewed in Nagy & Williams, 2001; Angelini & Kaufman, 2005b). In short, the leg is divided into three domains along the PD axis and patterned by genes with mutually exclusive gene expression domains. Loss of these gene expression domains causes loss of position-specific leg tissue and truncated or shortened legs. Experiments in *D. melanogaster* demonstrated that it was possible to partially duplicate the PD axis; manipulating signaling along the A-P boundary formed new sites of PD elongation and ultimately branched legs with duplicated distal axes (Struhl & Basler, 1993; Diaz-Benjumea et al., 1994). This led to the hypothesis that reiterating the PD patterning network along the A-P segment boundary could have generated naturally occurring, branched limbs (Campbell & Tomlinson, 1995).

EXISTING COMPARATIVE DATA

Based on the hypothesis above, limb patterning genes from *Drosophila melanogaster* were candidates to regulate limb patterning in other species. When *D. melanogaster* genes were examined in other species, both in expression and function, it became clear that, while some genes are expressed similarly across arthropods, the entire network from *D. melanogaster* was not conserved. Critically, the *wingless* and *decapentaplegic* genes that function directly upstream of PD elongation in *D. melanogaster* do not show conserved function, even within insects, and so cannot explain modulation of PD elongation (Angelini & Kaufman, 2005a, 2005b). PD elongation is based primarily on the activation of *Distal-less* in *D. melanogaster*. Although analyses of *Distal-less* function in other arthropods show that it is required for PD growth of limbs (Beerman et al., 2001; Shoppmeier & Damen, 2001; Khila & Grbic, 2007), there is no evidence that the PD patterning network is reiterated to form branches. Instead, in every case where it has been examined, the evidence points to a single PD patterning axis whether the limb has only one axis, a bifurcated axis, or is a highly modified paddle (Fig. 2G; Williams, 1998; reviewed in Williams & Nagy, 2001; Williams et al., 2002).

Indeed, the network of genes regulating PD outgrowth is broadly conserved.

WHAT IT DOES AND DOES NOT EXPLAIN

Two points in limb development appear broadly conserved with little variation. First, all limbs examined are positioned along the A-P segment boundary. In spite of this conserved positioning, the signaling that subsequently occurs along the A-P boundary that initiates PD outgrowth in *Drosophila melanogaster* is not conserved. Nevertheless, once it is initiated, the network of PD leg patterning and elongation is the second broadly conserved aspect of leg patterning. This appears to be the case even in limbs of highly divergent morphology, like the flattened, multilobed paddles of branchiopod crustaceans. The deep conservation of PD patterning is striking and probably represents a core set of genes that, once activated, can produce a limb (i.e., a limb-patterning module). However, one core aspect of variation in limbs, branches or outgrowths from the main axis, is not explained by the comparative data. The analysis of candidate genes yielded no patterns that gave rise to new hypotheses explaining branching, and we currently have no good working models to account for such limb variation.

The analysis of candidate genes from *Drosophila melanogaster* limb patterning is complicated by the fact that a number of genes involved in limb patterning have pleiotropic effects. For example, *Distal-less* protein is found in almost every appendage examined to date, but evaluating its role in patterning limb outgrowth is confounded by its additional role in sensory development (Mittmann & Scholtz, 2001; Williams et al., 2002; Williams, 2008). Although *Distal-less* is well known to function in the nervous system of *D. melanogaster* (Panganiban, 2000), its role in limb patterning is distinct both spatially and temporally because of *D. melanogaster*'s specialized metamorphic mode of development, where the segregation and patterning of cells fated to become limbs occur much earlier than the differentiation of limb sensory structures. Most arthropods lack this segregation between limb patterning and limb differentiation, and, therefore, gene expression regulating limb patterning overlaps gene expression regulating sensory patterning, confounding the inference of function in limbs with complex morphology.

CONCLUSIONS

EvoDevo promised to revive and answer some longstanding questions about the morphological diversity that results from adaptive radiations. How far has the paradigm of diversification using a finite toolkit taken us within the field of arthropod EvoDevo? With respect to the three areas analyzed herein, each feature shows surprising instances of deep conservation of certain patterning mechanisms. For tagmatization and limb identity along the A-P axis, *Hox* genes play a fundamental role in shifting the boundaries of limb morphology. For variation in segment number, *Notch* involvement is widespread. For limb morphology, there is a highly conserved PD patterning module.

The idea of a finite toolkit has proven to be a surprisingly robust hypothesis. In many cases, when we examine nonmodel organisms, we find the same regulatory genes in the same roles they play in model systems. Furthermore, some aspects of variability can be explained by changes in broadly conserved genes. For example, the subspecialization of limbs within tagma seems to be well modeled by shifts in the boundaries of *Hox* expression. However, what has also become clear is that there are two main drawbacks to following this approach. First, candidate genes may not be widely conserved or may have pleiotropic effects that complicate our modeling their roles. Second, and more profound, the level of patterning that is deeply conserved is often not the level that establishes the details of morphology that are fundamental to adaptive radiations. This is most clearly illustrated by the analysis of limbs. Whereas there does seem to be a widespread PD patterning module that forms a single PD axis in all limbs, we have no general models to explain the morphological variability that characterizes the functional diversification of limbs. Nor do we know how the limb axis is bifurcated in two-branched forms. Given that the branching and outgrowths of limbs are the very substrate of their functional diversity, this conserved patterning module has not served us well in analyzing that diversification.

Even as we write this, EvoDevo is being transformed by the development of new tools that in part address some of the limitations. Transgenesis and RNAi are transforming our ability to conduct functional studies in nonmodel arthropods. These methods will facilitate a much-needed wider taxon sampling. With RNAi, we can test gene function in nonmodel systems and test whether the assumptions derived from a few model systems hold more broadly. High-throughput sequencing/proteomics speed up gene discovery at an incredible rate and are limited only by financial resources rather than the life history strategies of an organism. The sequenced genomes confirm that the generic developmental toolkit is widely present. Interestingly, 30%–60% of open

reading frames identified in the arthropod species sequenced to date have no identifiable orthologs in other species, and as much as 50% of the active transcriptome in some species are these orphan genes. These orphan genes may have important functions in nonmodel systems. These new approaches are opening new windows on how genomes evolve. How directly those windows will lead to more a complex understanding of the kinds of changes that natural selection can act upon remains to be seen.

In addition to the increased use of genomics, transcriptomics, and proteomics to further our mechanistic understanding of development, several other parallel trends or research programs can be discerned (e.g., Müller, 2007). One is a trend toward using computational and bioinformatics approaches to understand development and how developmental processes evolve; another is the integration of ecological and environmental aspects of developmental biology into what is often called EcoDevo (Gilbert, 2001). In addition, evolution and development studies applied to smaller-scale evolutionary problems within insects have had success (e.g., Kopp, 2011; Prud'homme et al., 2011; Frankel et al., 2012). Finally, it is sometimes forgotten that another important trend is continued emphasis, especially in marine invertebrates (Love, 2009), on developing a phylogenetically informed comparative embryology.

We conclude that EvoDevo has made great strides in uncovering the common features underlying the development of morphology. The field has also made a start at the discovery of both protein and regulatory changes that correlate with morphological changes. At the same time, resolution of many longstanding questions about morphological diversity has largely not occurred. Arthropod morphological diversity is structurally complex and not often captured by broadly conserved patterning elements. The ultimate goal is to understand the complete arc from genetic regulation to expressed phenotype in a set of related organisms. This goal of understanding how the genotype translates into the complex, evolvable morphological phenotype remains for the future.

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OPTIMIZATION OF VIRUS-INDUCED GENE SILENCING TO FACILITATE EVO-DEVO STUDIES IN THE EMERGING MODEL SPECIES *MIMULUS GUTTATUS* (PHRYMACEAE)[1]

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ABSTRACT

Mimulus guttatus DC. (yellow monkey-flower; Phrymaceae) is an important model species for ecological and evolutionary studies, being locally adapted to a wide range of elevation, moisture and temperature gradients, soil types, and pollinator availabilities. In order to advance this species as a model for evolutionary genetic studies, we have developed virus-induced gene silencing (VIGS) using the tobacco rattle virus (TRV) to assay gene function. We demonstrate the effectiveness of *Agrobacterium*-mediated VIGS in two divergent populations of *M. guttatus*, Iron Mountain 767 (IM767) and Point Reyes (PR). Plants infected with a fragment of the carotenoid biosynthesis pathway gene *PHYTOENE DESATURASE* (*PDS*) cloned into the TRV2 vector exhibited endogenous *PDS* silencing and photobleached phenotypes. We further assayed for VIGS-induced floral phenotypes by silencing paralogous genes putatively affecting floral symmetry, *CYCLOIDEA1* (*CYC1*) and *CYCLOIDEA2* (*CYC2*). Simultaneous silencing of *CYC1* and *CYC2* resulted in organ number defects in the petal and stamen whorls; silencing of *CYC1* affected petal margin growth; and silencing of *CYC2* had no effect on flower development. Infection with TRV2 and TRV1 is significantly higher and more pervasive in the IM767 versus the PR population and is more efficient after vacuum infiltration. These results demonstrate the efficacy of VIGS for determining the function of developmental genes, including those involved in ecologically important reproductive traits.

Key words: *CYCLOIDEA*, *Mimulus*, Phrymaceae, *PHYTOENE DESATURASE* (*PDS*), reverse genetics, virus-induced gene silencing (VIGS).

The cosmopolitan plant genus *Mimulus* L. (Phrymaceae) comprises ca. 160 to 200 species, the majority of which are derived from two rapid radiations in western North America and Australia (Beardsley & Olmstead, 2002). Species of *Mimulus* occupy a vast range of habitats, from desert to alpine, and are phenotypically diverse in both reproductive and life history traits (Vickery, 1978; Beardsley et al., 2004; Angert & Schemske, 2005; Wu et al., 2008). For example, major differences in floral form are associated with multiple shifts in pollinators and changes in the relative importance of selfing versus outcrossing (Bradshaw & Schemske, 2003). Much of the ecological and morphological diversity within the genus is evident in the young, but genetically diverse, species complex *M. guttatus* DC. (yellow monkey-flower) (Kelly & Willis, 1998; Sweigart & Willis, 2003; Beardsley et al., 2004). Populations of the *M. guttatus* complex are locally adapted to a range of elevation, moisture and temperature gradients, soil types, and pollinator availability, making them an excellent system for ecological studies (Allen & Sheppard, 1971; Fishman et al., 2002; Hall & Willis, 2005; Wu et al., 2008). Recent development of genomic tools, including a near-complete genome sequence of *M. guttatus*, have further made *Mimulus* an exciting model group in which to test fundamental evolutionary questions related to speciation, adaptation, and macroevolution (Hall & Willis, 2006; Holeski & Kelly, 2006; Cooley & Willis, 2009; Ivey et al., 2009; Lowry et al., 2009; Wu et al., 2010).

In addition to genomic tools, the development of *Mimulus guttatus* for evolutionary developmental genetic ("evo-devo") studies requires transformational capabilities to assay gene function. This can either be accomplished through forward or reverse genetic

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approaches. One promising reverse genetic method for the rapid and transient (intragenerational) silencing of gene expression is virus-induced gene silencing (VIGS) (Baulcombe, 1999; Robertson, 2004; Purkayastha & Dasgupta, 2009; reviewed in Di Stilio, 2011). VIGS utilizes the RNA interference (RNAi) pathway of plants to target endogenous messenger RNA (mRNA) for degradation (Fagard & Vaucheret, 2000; Robertson, 2004). Specifically, *Agrobacterium*-mediated infection of plant cells with a modified viral vector, containing a plant gene of interest, results in the expression of double-stranded RNAs that are degraded in vivo by DICER-like enzymes (Hamilton & Baulcombe, 1999; Zamore et al., 2000). This results in short, interfering RNAs of 12 to 23 bp that form the template for further degradation of complimentary RNAs, including endogenous mRNAs (Hammond et al., 2000; Zamore et al., 2000).

VIGS has proven effective in a wide range of distantly related angiosperm taxa (Di Stilio, 2011), including the monocots *Brachypodium distachyon* (L.) P. Beauv. (purple false brome) (Demircan & Akkaya, 2010), *Hordeum vulgare* L. (barley) (Holzberg et al., 2002), orchids (Lu et al., 2007), *Triticum aestivum* L. (wheat) (Scofield et al., 2005; Tai et al., 2005; Scofield & Nelson, 2009), and *Zingiber officinale* Roscoe (culinary ginger) (Renner et al., 2009); the basal eudicots *Aquilegia vulgaris* L. (common columbine) (Gould & Kramer, 2007), *Eschscholzia californica* Cham. (California poppy) (Wege et al., 2007), *Papaver somniferum* L. (opium poppy) (Hileman et al., 2005), and *Thalictrum* sp. L. (meadow rue) (Di Stilio et al., 2010); the asterids *Antirrhinum majus* L. (snapdragon) (Preston & Hileman, 2010), *Nicotiana benthamiana* Domin (tobacco) (Kumagai et al., 1995), *Petunia hybrida* (Hook.) Vilm (petunia) (Spitzer et al., 2007), *Solanum lycopersicum* L. (tomato) (Liu et al., 2002), and *Spinacia oleracea* L. (spinach) (Sather et al., 2010); and the rosids *Arabidopsis thaliana* (L.) Heynh. (thale cress) (Burch-Smith et al., 2006; Pflieger et al., 2008; Igarashi et al., 2009), *Glycine max* (L.) Merr. (soybean) (Zhang et al., 2009), and *Medicago truncatula* Gaertn. (Grønlund et al., 2008). However, despite the generality of VIGS, it is clear that not all vectors are effective in all species and that protocol optimization is required to elicit efficient gene silencing in nonmodel taxa (Liu & Page, 2008; Di Stilio, 2011).

Here, we demonstrate the effective use of VIGS in two morphologically diverse populations, Point Reyes (PR) and Iron Mountain 767 (IM767), of the emerging model species *Mimulus guttatus* using constructs containing *PHYTOENE DESATURASE* (*PDS*) or paralogous *CYCLOIDEA*-like (*CYC*-like) genes. *PDS* is a functionally conserved plant gene that is involved in the carotenoid biosynthesis pathway that protects the chloroplast from photo-oxidation; *PDS* silencing causes a characteristic photobleaching phenotype under high light growth conditions (Demmig-Adams & Adams, 1992; Benedito et al., 2004; Hileman et al., 2005; Gould & Kramer, 2007). By contrast, *CYC*-like genes generally affect cell proliferation and expansion in the petal and stamen whorls, mainly in the dorsal region of the flower (Luo et al., 1996, 1999; Cubas et al., 1999; Feng et al., 2006; Busch & Zachgo, 2007; Broholm et al., 2008; Fambrini et al., 2011).

Materials and Methods

Construction of *Mimulus guttatus* TRV2 VIGS vector

RNA was extracted from *Mimulus guttatus* PR and IM767 material using the RNeasy Plant Mini Kit and RNase-Free DNase Set (Qiagen, Valencia, California), and complementary DNA (cDNA) was generated using the iScript cDNA Synthesis Kit (Bio-Rad, Hercules, California). *MgPDS* was amplified from cDNA of both *M. guttatus* populations using the conserved primers ALL.PDS-F (5′-TTGWATGCCAARYAARCCWG-3′) and ALL.PDS-R (5′-ACACTIAGMAGKGRRCTTCTGC-3′), which carry degeneracies in order to amplify *PDS* from a number of taxa in the Lamiales. *MgCYC1* and *MgCYC2* were amplified from IM767 cDNA using the primers MgCYC1.full.F (5′-ACATGATTCCTCATGGCTCTTCTC-3′) and MgCYC1.full.R (5′-ACTTGTGGTGATCCAAAATGGCAG-3′), and MgCYC2.full.F (5′-CAGTTACCTCCATCCTCAGGCAAC-3′) and MgCYC2.full.R (5′-ACTTGTGCTGGTCCAAAATAGCAC-3′). The resulting fragments were cloned separately into TOPO-TA 2.1 (Invitrogen, Carlsbad, California), and their identity was confirmed by sequencing with reference to the published genome sequence (<http://www.phytozome.net/mimulus>). Nested fragments of *MgPDS* (Fig. 1), *MgCYC1*, and *MgCYC2* were amplified with primers PDS-F-BamHI (5′-ATAGGATCCTTGCWATGCCAARYAARCCWGG-3′) and PDS-R-XhoI (5′-AGTCTCGAGACACTIAGMAGKGRRCTTCTGC-3′), MgCYC1.VIGS.BamHIF (5′-ATAGGATCCGCAGCAAAGTAATAACCCTTCG-3′) and MgCYC1.VIGS.XhoIR (5′-AGTCTCGAGTCCTTCGAACCAGCTCCTTTAC-3′), and MgCYC2.VIGS.KpnIF (5′-AGTGGTACCCGGCATTGCTAGAAAGTTCTTC-3′) and MgCYC2.full.R to generate 5′ and 3′ restriction enzyme recognition sites. The resulting polymerase chain reaction (PCR)

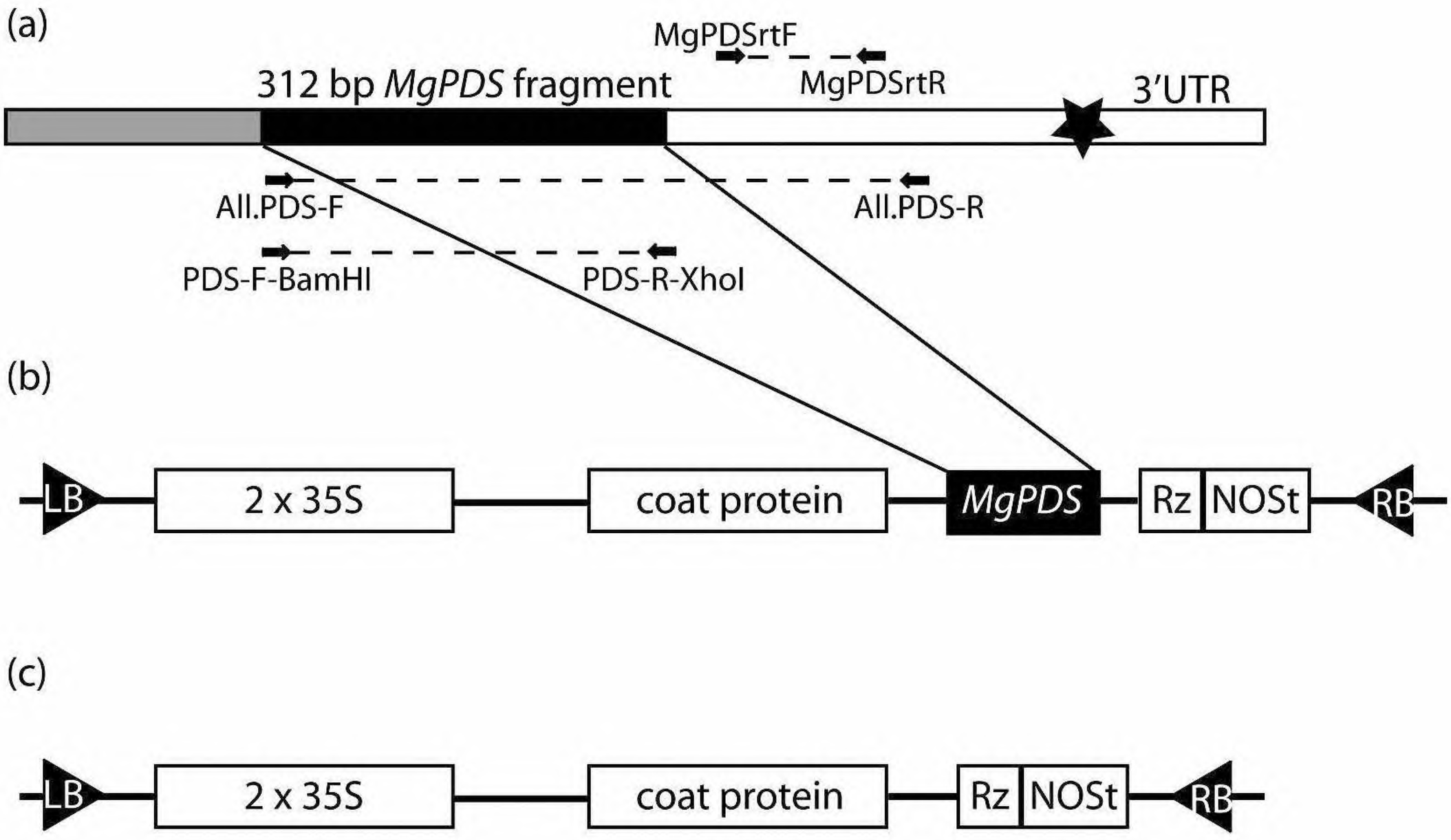


Figure 1. Example VIGS constructs. —A. Structure of *MgPDS* showing the 312 bp fragment (black) cloned into TRV2, the 5′ (gray) and 3′ (white) ends, and the position of the stop codon (star). Primer pairs used for amplification and sequencing are shown with arrows and dashed lines. —B. Map of the *MgPDS*-TRV2 construct used for VIGS. —C. Map of the Empty-TRV2 construct used as an experimental control. LB, left border; RB, right border; Rz, self-cleaving ribozyme; NOSt, NOS terminator.

fragments were digested with *Bam*HI and *Xho*I (*PDS* and *MgCYC1*), or *Kpn*I and *Xho*I (*MgCYC2*) and subcloned individually or together (*MgCYC1* and *MgCYC2*) into the tobacco rattle virus 2 (TRV2) vector digested with the same enzymes (Fig. 1).

ELECTROPORATION OF *AGROBACTERIUM TUMEFACIENS* WITH MODIFIED TRV2

To optimize infection of *Mimulus guttatus*, *MgPDS*-TRV2, or Empty-TRV2, and TRV1 were used to electroporate two strains of *Agrobacterium tumefaciens* Smith & Townsen (GV3101 and EHA105) (Dinesh-Kumar et al., 2003; Hileman et al., 2005). *Agrobacterium tumefaciens* was prepared according to a modified protocol (Hileman et al., 2005). Single colonies were used to inoculate 5 mL Luria Broth (LB) and were screened for the presence of the appropriate plasmids using primers pYL156F/pYL156R (TRV2 constructs) and OYL195/OYL198 (TRV1) as previously described (Hileman et al., 2005). PCR-positive cultures were used to inoculate 500 mL LB and were grown to an absorbance at 260 nm (Abs_{260}) of seven to nine. Pelleted cultures were resuspended in infiltration media (Hileman et al., 2005) to a final Abs_{260} of two, incubated for four to 12 hr. at room temperature, and used to inoculate *M. guttatus* PR and IM767 seedlings. After optimization of VIGS, *MgCYC1*-TRV2, *MgCYC2*-TRV2, and *MgCYC1:MgCYC2*-TRV2 were used to electroporate EHA105 as described.

SEEDLING INOCULATION WITH VIGS CONSTRUCTS

Mimulus guttatus seedlings were grown to the two to three leaf pair stage at 20°C–22°C under long-day (16 hr. light/8 hr. dark) conditions on a 1:1 mix of vermiculite and soil. One hundred to 200 seedlings were inoculated with a 1:1 ratio of *Agrobacterium tumefaciens* GV3101 or EHA105 carrying TRV1 and *MgPDS*-TRV2, or Empty-TRV2 per treatment as previously described (Hileman et al., 2005). Batches of 50 *M. guttatus* PR and IM767 seedlings were subjected to four different inoculation treatments: 1 min. vacuum infiltration, 3 min. vacuum infiltration, 15 min. submersion without vacuum, and injection of leaves with a needleless syringe. Inoculated seedlings were replanted in soil and grown for an additional two (IM767) to four (PR) weeks at 20°C–22°C before leaf tissue was collected for RNA extraction. Differences in tissue harvest times were based on interpopulation variation in phenotype emergence. All surviving plants were examined for evidence of photobleaching as well as any obvious differences in flowering time and flower development relative to wild type. Once conditions had been optimized, VIGS was carried out as previously described in approximately 200 IM767 seedlings using the *MgCYC1*-TRV2, *MgCYC2*-

TRV2, or *MgCYC1:MgCYC2*-TRV2 construct with 1 min. vacuum infiltration.

RNA EXTRACTION AND GENE EXPRESSION ANALYSIS

Leaf tissue from surviving plants was harvested and pooled per five to 10 individual plants, and total RNA was extracted using TriReagent (Applied Biosystems, Foster City, California). For each RNA pool, 1 μg was reverse transcribed using the iScript cDNA Synthesis Kit (Bio-Rad). cDNA was diluted 1:10 and 2 μL was used as a PCR template to screen for the presence of TRV2 and TRV1 plasmids as previously described (Hileman et al., 2005). After identification of infected pools, total RNA was extracted from leaves of individual plants. cDNA was then synthesized after DNA digestion with TURBO DNA-free (Applied Biosystems), and each cDNA was screened for presence of TRV2 and TRV1. *ACTIN* was amplified for 28 cycles as an internal control as described in Prasad et al. (2001).

To determine if a reduction in *PDS* levels was correlated with photobleaching, a ca. 150 bp region of *PDS* was amplified from cDNA of green leaf RNA harvested from Empty-TRV2-infected and uninfected individuals, and white leaf RNA harvested from *MgPDS*-TRV2-infected individuals. MgPDSrt-F (5′-CGAAGATGGCATTTTTGGAT-3′) and MgPDSrt-R (5′-ATGGCATCTCTTTCCATTCG-3′) were designed in Primer3 (Rozen & Skaletsky, 2000) to amplify a region downstream of the VIGS *PDS* insert region, and PCRs were run for 28, 30, and 32 cycles to confirm linearity. *MgPDS* expression levels were normalized against *ACTIN* in ImageJ (Abramoff et al., 2004) with two to six biological replicates.

Silencing of *MgCYC1* and *MgCYC2* was determined using quantitative (q) reverse transcriptase (RT)-PCR. The *MgCYC1* primers MgCYC1.rt.new.F (5′-CGAACAACGGGAAATTATGC-3′) and MgCYC1.rt.new.R (5′-GCCGTAGTTGGAACTCGAAA-3′), and the *MgCYC2* primers MgCYC2.rt.new.F (5′-CGGCCCGTCTGCTAATAAT-3′) and MgCYC2.rt.new.R (5′-CCTATTGATGAACTTGGCTGGT-3′) were designed to amplify a 150 bp fragment downstream of the VIGS construct sequence in Primer3 (Rozen & Skaletsky, 2000). Primer efficiency was determined using Fast SYBR Green Master Mix (Life Technologies) as previously described (Preston & Hileman, 2010). After correcting for transcriptional stability, cycle threshold values were normalized against the housekeeping gene *EF1alpha* as previously described (Scoville et al., 2011), and the mean was calculated for four technical replicates. Flowers positive for *MgCYC1*-TRV2, *MgCYC2*-TRV2, and *MgCYC1:MgCYC2*-TRV2 were examined for organ number, shape, and identity, and compared to wild type flowers.

Results and Discussion

PHOTOBLEACHING IN MGPDS-TRV2 VIGS TREATED PLANTS

Silencing of *PDS* causes a characteristic photobleached phenotype that can be easily screened by the naked eye (Benedito et al., 2004; Hileman et al., 2005). To compare the efficiency of VIGS for the two populations of *Mimulus guttatus*, we attempted to infect plants with two *Agrobacterium tumefaciens* strains, using four different treatments. Each *MgPDS*-TRV2-treated plant was then screened for evidence of photobleaching. For the PR population, *MgPDS*-TRV2-treated seedling survival ranged from 68% to 84% using GV3101 and 3% to 29% using EHA105, with the highest survival rate for the 3 min. vacuum infiltration treatment for both *A. tumefaciens* strains (Table 1). Photobleached plants were identified in all but the leaf injection treatment for both GV3101 and EHA105. For the three successful treatments using GV3101 (1%–6%), the percentage of photobleached survivors was significantly higher (6%) after 3 min. vacuum infiltration (Table 1). This trend was also observed using EHA105. However, treatments using EHA105 were less efficient (0%–3% infected) than GV3101 (Table 1). Furthermore, for all plants showing a phenotype, photobleaching was only observed on one or two leaves (Fig. 2A, B); no photobleaching was observed in reproductive tissues.

Similar to the PR population, no photobleaching was observed for the leaf injection treatment in IM767. Furthermore, unlike the PR population, IM767 seedlings were unable to survive 3 min. vacuum infiltration regardless of the *Agrobacterium* strain used. For the other two treatments, survival ranged from 25% (1 min. vacuum; EHA105) to 40% (15 min. dip; both *Agrobacterium* strains). However, photobleached individuals were only found after 1 min. vacuum infiltration. The efficiency of *MgPDS*-TRV2 VIGS using GV3101 (3%) was similar to the most efficient treatments in the PR population. By contrast, 1 min. vacuum infiltration using EHA105 was significantly higher in the IM767 population (24%) versus the PR population (Table 1). This level of VIGS efficiency is similar to that found for *PDS* silencing in *Papaver* L. using EHA105 (Hileman et al., 2005) and *Aquilegia* L. using GV3101 (Gould & Kramer, 2007); VIGS has been successfully used in both these species to elucidate the function of flower developmental genes (Drea et al., 2007; Kramer et al., 2007; Yellina et al., 2010; Hands et al., 2011).

Table 1. Survival and infection rates for VIGS-treated *Mimulus guttatus* DC. seedlings.

	Point Reyes				Iron Mountain 767			
Agrobacterium strain	1 min.	3 min.	3 min.	15 min.	1 min.	1 min.	3 min.	15 min.
GV3101								
Construct	PDS	E	PDS	PDS	E	PDS	PDS	PDS
N treated	150	100	100	200	100	100	100	100
Survival (%)	68	60	84	67	40	34	0	40
Survivors infected (%)	2	0	6	1	0	3	N/A	0
Phenotype[1] (%)	2	0	6	1	0	3	N/A	0
EHA105								
Construct	PDS	E	PDS	PDS	E	PDS	PDS	PDS
N treated	150	100	100	150	100	150	100	100
Survival (%)	3	24	29	24	21	25	0	40
Survivors infected (%)	0	0	3	0	14	24	N/A	0
Phenotype[1] (%)	0	0	3	0	0	24	N/A	0

Abbreviations: PDS, *MgPDS*-TRV2; E, Empty-TRV2.
[1] Percentage of survivors.

Furthermore, ca. 50% of the IM767 plants showing a phenotype were almost completely photobleached (Fig. 2D, E). This level of photobleaching caused severe retardation (Fig. 2D, E), followed by death prior to development of the reproductive organs. Consequently, no photobleaching was observed in reproductive structures.

To confirm that photobleaching in both *Mimulus guttatus* populations was positively correlated with *MgPDS*-TRV2 and TRV1 infection, and was not a result of infection per se, tissues from both *MgPDS*-TRV2- and Empty-TRV2-treated plants were PCR screened for the presence of TRV2 and TRV1. For both the PR and IM767 populations, all photobleached leaves were infected with both *MgPDS*-TRV2 and TRV1 (Fig. 3A); no green leaves were positive for either vector. Control plants positive for both Empty-TRV2 and TRV1 were only found in the IM767 population using EHA105 (14%), consistent with infection rates for *MgPDS*-TRV2 (Table 1; Fig. 3A). None of these infected control plants showed photobleaching in vegetative or reproductive tissues, and growth was normal throughout development. Thus, photobleaching was correlated with *MgPDS*-TRV2 infection, rather than viral infection per se. Furthermore, all Empty-TRV2-treated plants that screened positive for the virus in leaves also screened positive in flowers, suggesting that infection remains into the reproductive stage of development.

PDS TRANSCRIPT LEVELS IN PHOTOBLEACHED *MIMULUS GUTTATUS* PLANTS

To verify that photobleaching in *MgPDS*-TRV2-infected plants correlated with reduced endogenous *MgPDS* transcript levels, we performed RT-PCR on both PR and IM767 plants infected with *MgPDS*-TRV2 in GV3101 and EHA105, IM767 plants infected with Empty-TRV2 in EHA105, and plants from the same treatments that were not infected. For each infected plant, endogenous *MgPDS* expression levels were calculated relative to uninfected plants from the same treatment (set to an expression level of 1) after standardization against *ACTIN* (Fig. 3B). RT-PCR analyses confirmed silencing of endogenous *MgPDS* in *MgPDS*-TRV2 plants relative to both uninfected and Empty-TRV2 control plants (Fig. 3B). For both GV3101 and EHA105 treatments, average silencing was two-fold with a high level of variation between individuals, ranging from no significant silencing to 10-fold silencing (Fig. 3B). Because whole leaves were harvested for expression analyses, inter-individual variation in endogenous *MgPDS* expression is most likely due to differences in the number of leaf cells infected with *MgPDS*-TRV2. The amount of photobleaching per *MgPDS*-TRV2-infected individual ranged from small sectors on individual leaves (GV3101 in PR) to complete photobleaching of one or two leaves (EHA105 in PR and IM767) to almost complete photobleaching of the whole seedling (EHA105 and GV3101 in IM767) (Fig. 2A, B, D, E). This level of VIGS photobleaching variation is consistent with reports from other species (Hileman et al., 2005; Liu & Page, 2008).

TRANSCRIPT SILENCING OF PUTATIVE FLORAL *CYC* SYMMETRY GENES

The fact that *Mimulus guttatus* IM767 infection persists into flowers (previous section) suggests efficacy of VIGS in reproductive tissues. However, in order to verify that infection of reproductive tissues

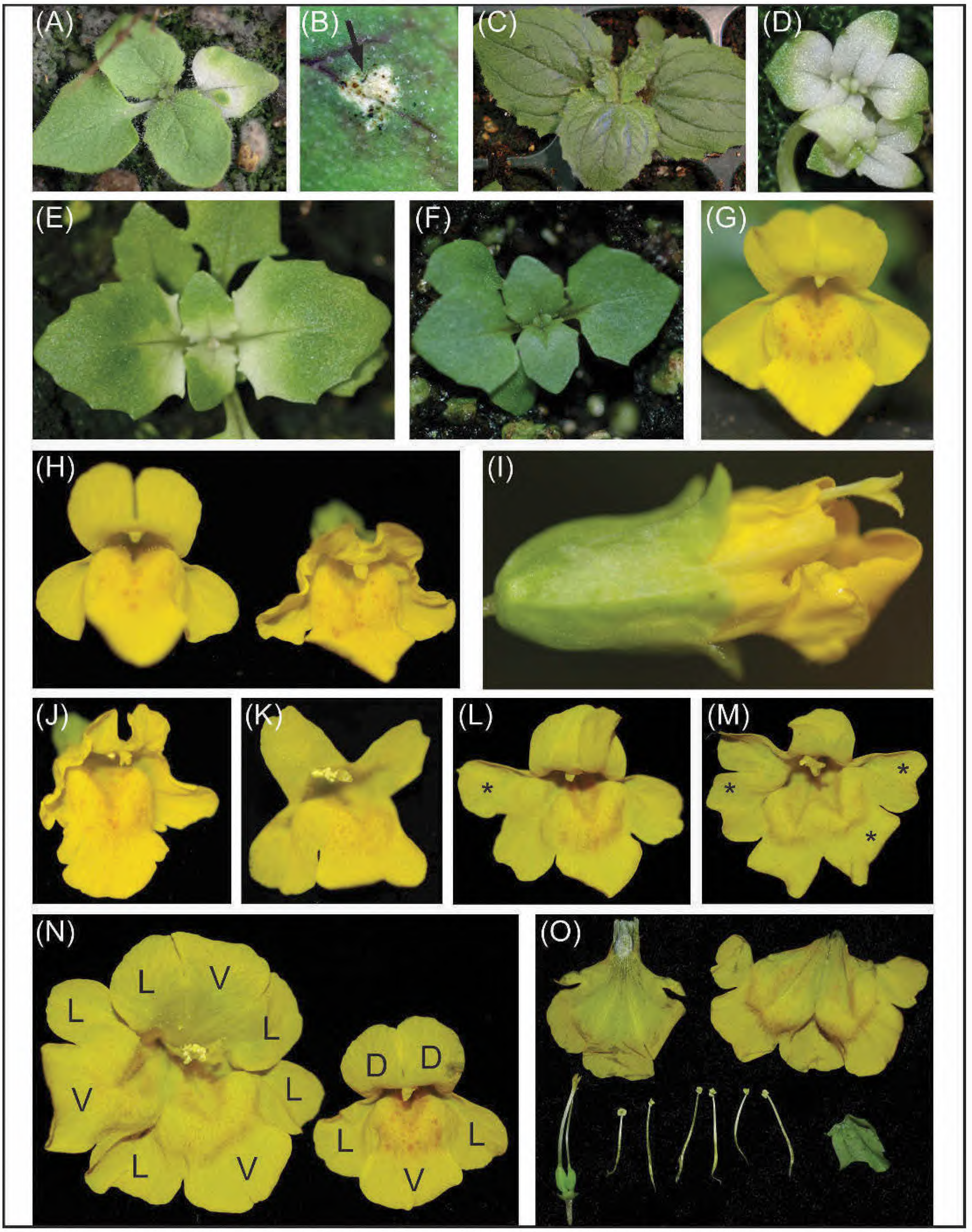


Figure 2. Variation in leaf photobleaching and flower morphology for *MgPDS*-TRV2- and *MgCYC*-TRV2-infected plants. A, B. Infected plants of *Mimulus guttatus* PR treated with *MgPDS*-TRV2 in GV3101 show variation in the extent of photobleaching [arrow in (B)] in individual leaves. —C. Uninfected *M. guttatus* PR plants treated with *MgPDS*-TRV2 show no sign of photobleaching. —D. Almost completely photobleached *MgPDS*-TRV2 in EHA105-infected *M. guttatus* IM767 seedling. —E. Initial stages of systemic photobleaching for an *MgPDS*-TRV2 in GV3101-infected *M. guttatus* IM767 seedling. —F. Uninfected *M. guttatus* IM767 plants treated with *MgPDS*-TRV2 show no sign of photobleaching. —G. Empty-TRV2 positive flower showing wild type morphology. —H. *MgCYC1*-TRV2-infected flowers (right) have small dorsal petal and wavy petal margins compared to uninfected flowers (left). —I. Infected flower in H. Infected flower prior to anthesis has shortened dorsal petals, resulting in protrusion of the stigma. —J. Another example of an *MgCYC1*-TRV2-infected flower showing wavy margins in all petals. K–M. *MgCYC1:MgCYC2*-TRV2-infected flowers have an abnormal number of lateral and/or ventral

also causes gene silencing and has a correlated effect on phenotype, we silenced two homologs of the *Antirrhinum majus* clade II TCP family flower symmetry genes *CYCLOIDEA* (*CYC*) and *DICHOTOMA* (*DICH*) (Luo et al., 1996, 1999). In *A. majus*, mutations in *CYC* result in partial loss of dorsal petal and staminode identity, resulting in plants with five fully developed stamens and partially radialized petals (Luo et al., 1996, 1999). By contrast, the *dich* mutant has no effect on stamen number but causes the loss of internal asymmetry within the dorsal petals; loss-of-function mutations in both *CYC* and *DICH* result in fully radialized flowers that have six ventral petals and six ventral stamens (Luo et al., 1996, 1999).

Of the IM767 seedlings vacuum infiltrated for 1 min. with the *MgCYC* gene-silencing constructs, three (6% of survivors), five (28% of survivors), and six (15% of survivors) individuals had flowers that were positive for *MgCYC1*-TRV2, *MgCYC2*-TRV2, and *MgCYC1:MgCYC2*-TRV2, respectively. Q-RT-PCR analyses of gene expression revealed that *MgCYC1* expression was significantly reduced in *MgCYC1*-TRV2 and *MgCYC1:MgCYC2*-TRV2-infected versus uninfected flowers collected for RNA post-anthesis (Fig. 3C). Similarly, *MgCYC2* expression was significantly reduced in *MgCYC2*-TRV2 and *MgCYC1:MgCYC2*-TRV2-infected versus uninfected post-anthesis flowers (Fig. 3C). This demonstrates that gene silencing was target specific. In the case of *MgCYC2*-silenced flowers, no abnormal phenotype was detected relative to uninfected plants in terms of organ number, size, shape, or identity. By contrast, infection and partial silencing of *MgCYC1*, and *MgCYC1* and *MgCYC2* together was correlated with abnormal petal and/or stamen whorl phenotypes but did not affect sepal morphology (Fig. 2H–O).

All nine *MgCYC1*-TRV2-infected flowers from three plants had petals with wavy margins compared to the smooth margins of wild type and Empty-TRV2-infected flowers (Fig. 2G–J). In each case, this growth defect was found in dorsal, lateral, and ventral petals (Fig. 2H–J). In addition to wavy petal margins, the two dorsal petals of infected flowers appeared shortened relative to wild type dorsal petals and infected lateroventral petals (Fig. 2H–J). Quantitative analyses of flower size revealed that *MgCYC1*-TRV2-infected flowers were shorter and narrower than uninfected flowers (Fig. 3D, E). Furthermore, the average ratio between dorsal and ventral petal lobe length was smaller in *MgCYC1*-TRV2-infected relative to uninfected flowers (Fig. 3F). This suggests that the reduction in growth was more extreme for dorsal petals than for ventral petals. Indeed, in some cases, reduction of dorsal petal size was evident at the bud stage (Fig. 2I); in wild type flower buds, the dorsal petals enclose the reproductive structures, whereas in two *MgCYC1*-TRV2-infected flowers, the anthers and stigma protruded from the flower bud.

In striking contrast to *MgCYC1*- and *MgCYC2*-silenced flowers, all *MgCYC1:MgCYC2*-TRV2-infected flowers had extra petals and/or stamens relative to wild type and Empty-TRV2-infected flowers (Figs. 2L–O, 3G). In wild type *Mimulus guttatus* plants, five stamen primordia give rise to two lateral and two ventral stamens and a single dorsal staminode that arrests growth in early development (pers. obs.). By contrast, in *MgCYC1:MgCYC2*-TRV2-infected flowers, one or two stamens developed in the dorsal region, resulting in a total of five to six pollen-producing stamens at anthesis (Figs. 2M, 3G). This gene-silenced phenotype is similar to *cyc* and *cyc:dich* mutants of *Antirrhinum majus*, which develop five and six stamens, respectively, compared to four stamens and one dorsal staminode of wild type flowers (Luo et al., 1996, 1999). In addition to stamens, *MgCYC1:MgCYC2*-TRV2-infected flowers showed organ number and identity defects in the petal whorl. Infected flowers ranged from having one less lateral petal to having both extra lateral and ventral petals (Figs. 2K–O, 3G). In the most extreme case, flowers were almost fully radialized due to the development of three sets of two lateral and one ventral petal. The flowers of this plant also had six stamens and showed a novel phenotype consisting of two instead of one gynoecium (Fig. 2N, O).

DIVERGENCE OF *CYC* GENE FUNCTION IN ASTERIDS

MgCYC1 and *MgCYC2* are the closest homologs of *CYC* and *DICH* from *Antirrhinum majus*, falling into the ECE CYC2 clade of TCP genes (Howarth & Donoghue, 2006). However, the duplication events that gave rise to the ECE CYC2 clade paralogs of *Mimulus guttatus* and *A. majus* occurred independently. Thus, comparison of these genes in asterids can inform our understanding of functional diversification after gene duplication. The VIGS data

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petals (asterisks). —N. Comparison of an extreme *MgCYC1:MgCYC2*-TRV2-silenced floral phenotype (left) with that of an uninfected flower (right). —O. Dissected flower from (N) showing an increase in stamen, petal, and gynoecium number. In addition to a doubling of the lateroventral petal unit in the ventral domain, the dorsal petals are partially transformed into a dorsal lateroventral-like unit. D, dorsal; L, lateral; V, ventral.

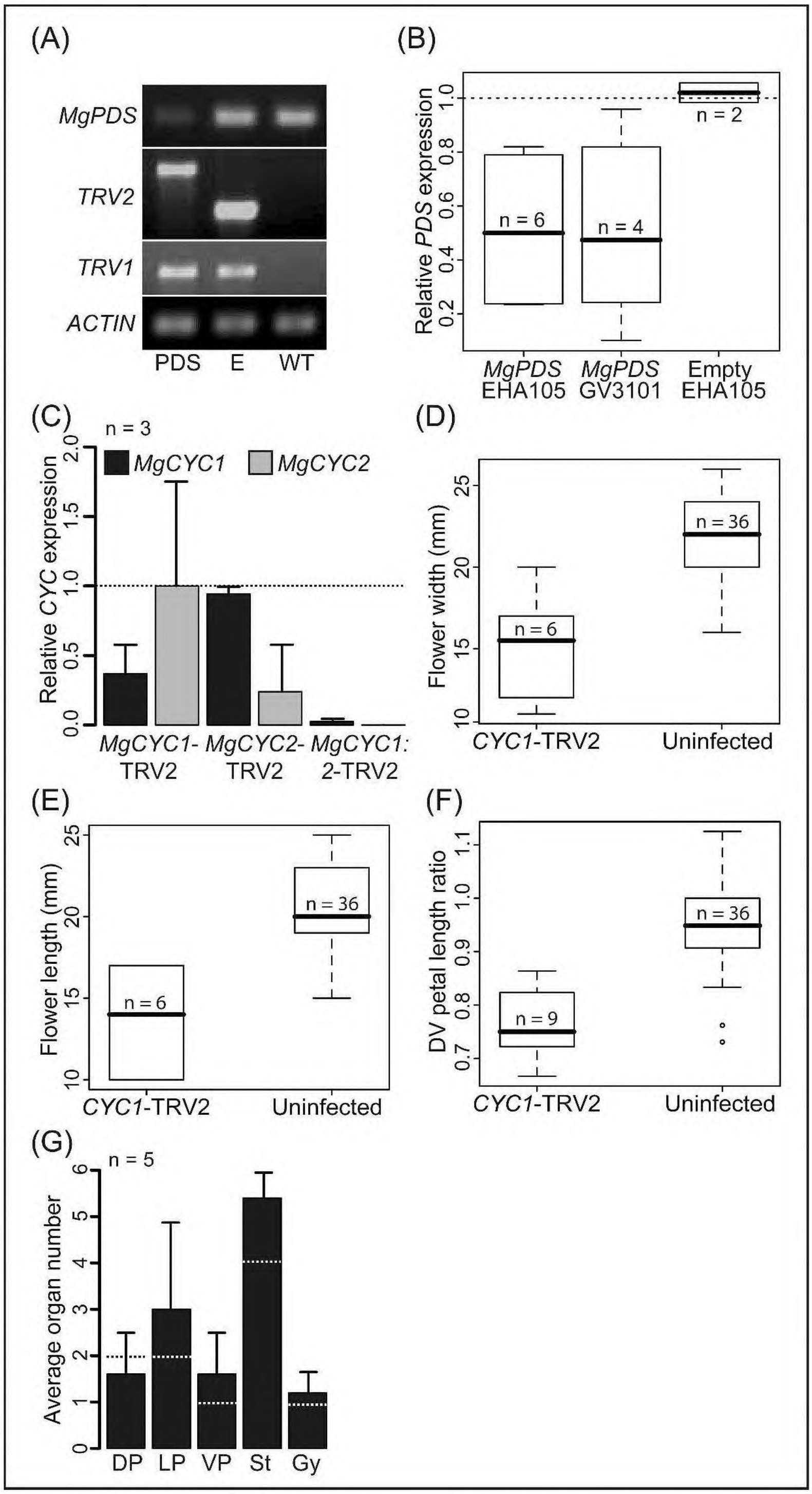


Figure 3. VIGS-mediated silencing of *PDS* and *CYC* genes. —A. RT-PCR showing the presence of TRV vectors in two representative IM767 individuals infected with *MgPDS*-TRV2 (*PDS*; larger TRV2 band) and Empty-TRV2 (E; smaller TRV2 band). These screening methods were used to determine the number of infected individuals described in Table 1. Endogenous levels of *MgPDS* are reduced in individuals infected with *MgPDS*-TRV2 relative to Empty-TRV2-infected and uninfected individuals. *ACTIN* was amplified as an internal control. —B. Boxplots showing variation in *ACTIN*-standardized endogenous *MgPDS* expression levels relative to the average of two to four uninfected individuals (dotted line) for each population and

presented in this paper support both similar and divergent functions for *MgCYC1* and *MgCYC2* in flower development and suggest differential sub- and neo-functionalization of paralogous genes after independent duplications in Plantaginaceae (*A. majus*) and Phrymaceae (*M. guttatus*).

In the case of *MgCYC1*, silencing has an effect on dorsal petal size, consistent with the known function of TCP genes on dorsal petal development and cell proliferation (Luo et al., 1996, 1999; Feng et al., 2006; Busch & Zachgo, 2007; Broholm et al., 2008; Preston & Hileman, 2009; Kieffer et al., 2011; Bai et al., 2012; Braun et al., 2012). However, within the ECE CYC2 clade, the specific phenotype observed in *MgCYC1*-silenced flowers is unique to *Mimulus guttatus*. In *Antirrhinum majus*, mutations in either *CYC* or *DICH* have negative effects on dorsal petal growth, but mutations in *CYC* have positive effects on stamen growth. Furthermore, lateral petals of double *cyc:dich* mutants are transformed into ventral petals, and both petal and stamen number is increased (Luo et al., 1996, 1999). A role in dorsal identity is also suggested for species in the Commelinaceae, Poaceae, Malpighiaceae, Caprifoliaceae, Gesneriaceae, and Papaveraceae based on gene expression data (Damerval et al., 2007; Song et al., 2009; Yuan et al., 2009; Zhang et al., 2010; Howarth et al., 2011; Preston & Hileman, 2012).

Similar to *Antirrhinum majus cyc* mutants, silencing of *MgCYC1* negatively affects dorsal petal growth. However, like *A. majus dich* mutants, *Mimulus guttatus* dorsal petals are not transformed into lateral or ventral petals, and there is no effect on floral organ number. *MgCYC1* silencing also causes growth defects at the margins of dorsal, lateral, and ventral petals; this phenotype is so far novel to loss-of-function ECE CYC2 clade genes. Interestingly, a similar phenotype was recently observed when several distantly related *CINCINATTA*-like (*CIN*-like) TCP genes were simultaneously silenced (Koyama et al., 2011). Given the lack of this phenotype in Plantaginaceae and Asteraceae *CYC*-like mutant backgrounds, it is most parsimonious to infer the recent acquisition of petal margin growth function in the *MgCYC1* lineage. However, it is unclear why this phenotype was not observed in *MgCYC1:MgCYC2*-TRV2-infected plants. Our working hypothesis is that the loss of competition between *MgCYC1* and *MgCYC2* for protein partners may have resulted in a gain of function phenotype; this remains to be tested.

Although silencing of *MgCYC2* in a few *Mimulus guttatus* flowers resulted in no abnormal phenotypes, the observation that double *MgCYC1:MgCYC2*-TRV2-infected flowers on average had more petals and stamens than single gene-silenced flowers suggests that *MgCYC1* and *MgCYC2* have a redundant role in specifying dorsal identity and stabilizing organ number. A similar role has been assigned to *CYC* and *DICH* and is suggested for other asterid *CYC*-like genes (Luo et al., 1996, 1999; Cubas et al., 1999; Gao et al., 2008; Song et al., 2009; Preston et al., 2009, 2011; Fambrini et al., 2011). However, the fact that *MgCYC1:MgCYC2*-TRV2-infected flowers tend to duplicate the later-oventral petals as a single unit tentatively suggests differential integration of the petal module in asterids. This hypothesis warrants further investigation in the future.

Conclusion

By applying different treatments to two ecologically and morphologically distinct populations, we have optimized VIGS as a reverse genetics tool to assay protein function in *Mimulus guttatus*. Specifically, *Agrobacterium tumefaciens* EHA105-mediated treatments of IM767 seedlings at the two to three leaf pair stage, via 1 min. vacuum infiltration, proved highly efficient. This treatment of IM767 seedlings yielded ca. 14%–24% infected survivors, the majority of which carried the virus in all tissues throughout development (Table 1). In the case of infection with *MgPDS*-TRV2, systemic infection caused severe photobleaching, resulting in death prior to flowering. Thus, it was not possible to determine the ability of the virus to infect reproductive tissues. By contrast,

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treatment. Endogenous *MgPDS* levels are reduced in *MgPDS*-TRV2-infected individuals, but not Empty-TRV2-infected controls, relative to uninfected individuals using both EHA105 and GV3101 *Agrobacterium* strains. Data for *MgPDS*-TRV2-infected individuals include both the PR and IM767 populations; Empty-TRV2-infected individuals are from the IM767 population only. Solid horizontal line, median; box, interquartile range; whiskers, extending to the further point that is within 1.5× the interquartile range from the box. —C. Quantitative-RT-PCR expression data for *MgCYC1* (black bars) and *MgCYC2* (gray bars) in uninfected and *MgCYC1:MgCYC2*-TRV2-infected flowers post-anthesis. Data are averages for three biological replicates. Error bars denote standard deviations. —D. Effect of *CYC1* silencing on flower width. —E. Effect of *CYC1* silencing on flower height. —F. Effect of *CYC1* silencing on the ratio of dorsal to ventral (DV) petal lobe length. —G. Effect of simultaneous *CYC1* and *CYC2* silencing on organ number. Lateral petal (LP), ventral petal (VP), stamen (St), and gynoecium (Gy), but not dorsal petal (DP), numbers are all increased relative to uninfected control plants (dotted line). Error bars denote standard deviations.

screening for both TRV2 and TRV1 in individuals infected with the Empty-TRV2 control vector revealed 100% retention of the virus in flowers, without any effect on flowering time, vegetative and inflorescence development, or seed set. The efficacy of VIGS in flowers was verified by the silencing of two *CYC*-like homologs, resulting in wavy petal margins, reduced dorsal petal growth, extra lateroventral petals and stamens, and variable loss of dorsal identity. Together, these data demonstrate the potential of VIGS as a fast and reliable method to assay gene function in *M. guttatus*, advancing this species further as a tool for addressing fundamental ecological and evolutionary questions.

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THE MADS-BOX GENE FAMILY OF THE BASAL EUDICOT AND HYBRID *AQUILEGIA COERULEA* 'ORIGAMI' (RANUNCULACEAE)[1]

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ABSTRACT

The MADS-box genes form a large family of pan-eukaryotic transcription factors that are involved in various aspects of plant growth and development, particularly reproduction. To understand the extent of their conservation and divergence in the emerging model genus *Aquilegia* L. (Ranunculaceae), we have annotated 47 MADS-box containing loci from the recently released hybrid *A. coerulea* E. James 'Origami' genome sequence. Phylogenetic analysis of these sequences along with those previously identified from *Arabidopsis* (DC.) Heynh. and *Oryza* L. demonstrates that we were able to recover members of all major subfamilies with the exception of clear Mβ representatives. The evolution of the *Aquilegia* type I loci is similar to what has been observed for other angiosperms in exhibiting relatively recent gene radiation events. In contrast, the type II loci are distributed across 12 subfamilies that were established before the diversification of the angiosperms. Overall, expressed sequence tag (EST) data exist for 20 of these loci; further characterization of gene expression patterns will be an important next step. This characterization of *Aquilegia* MADS-box transcription factors thereby lays the foundation for many crucial studies on the development and evolution of *Aquilegia* as well as the conservation of function across the MADS-box gene family.

Key words: *Aquilegia*, gene duplication, MADS-box genes, Ranunculaceae.

The MADS-box family of transcription factors is well known for regulating growth and developmental processes across eukaryotes, but it appears to be especially critical in plants (Messenguy & Dubois, 2003; Gramzow & Theissen, 2010). Members of the family are defined by the presence of the conserved MADS-box, which is typically located at or close to the 5′ end of the coding region and consists of a 180 bp motif. This sequence encodes a DNA-binding domain that recognizes regulatory elements known as CArG boxes, which have the consensus sequence 5′CC[A/T]$_6$GG-3′ (Riechmann et al., 1996b). Although MADS-box genes are found in animals, fungi, and plants, they tend to be much more diverse in plants, particularly seed plants (Nam et al., 2003; Gramzow & Theissen, 2010). Broadly speaking, there are two main evolutionary lineages of MADS-box genes, which are referred to as type I and type II (Fig. 1). The better-studied type II lineage includes MEF2-like genes in animals and fungi and MIKC-type genes in plants (Alvarez-Buylla et al., 2000). The MIKC-type genes derive their name from the four conserved domains defined in their protein sequences: MADS (M), Intervening (I), Keratin-like (K), and C-terminal (C) (Ma et al., 1991). MIKC-type genes can be further subdivided into the MIKC^C and MIKC* (or Mδ) types, of which the MIKC^C-type are the best-characterized group of MADS-box genes (Gramzow & Theissen, 2010). Numerous studies have demonstrated that MIKC^C MADS-box genes function as dimers and in higher-order protein complexes (reviewed in Gramzow & Theissen, 2010). These protein–protein interactions are primarily mediated by α-helical regions of the K domain with some contributions from the I and MADS domains (Riechmann et al., 1996a; Yang et al., 2003; Yang & Jack, 2004). In contrast to the well-understood M, I, and K domains, the C-terminal domain shows much lower levels of sequence conservation overall and remains somewhat of a mystery. Several subfamilies of MIKC^C loci contain transcriptional activation domains at their C-terminus (Honma & Goto, 2001), but no functions have been clearly ascribed to the highly conserved C-terminal motifs that define each lineage of the MIKC^C subfamily (reviewed in Litt & Kramer, 2010). Of the 14 major angiosperm lineages of MIKC^C loci, 11 contribute directly to the transition to flowering or the development of flowers themselves (reviewed in Yant et al., 2009; Gramzow & Theissen, 2010; Melzer et al., 2010), making comparative studies of this group of particular importance for understanding the evolution of flowering plants. The MIKC*-type were originally found in mosses and clubmosses but have now also been identified in well-studied seed plants

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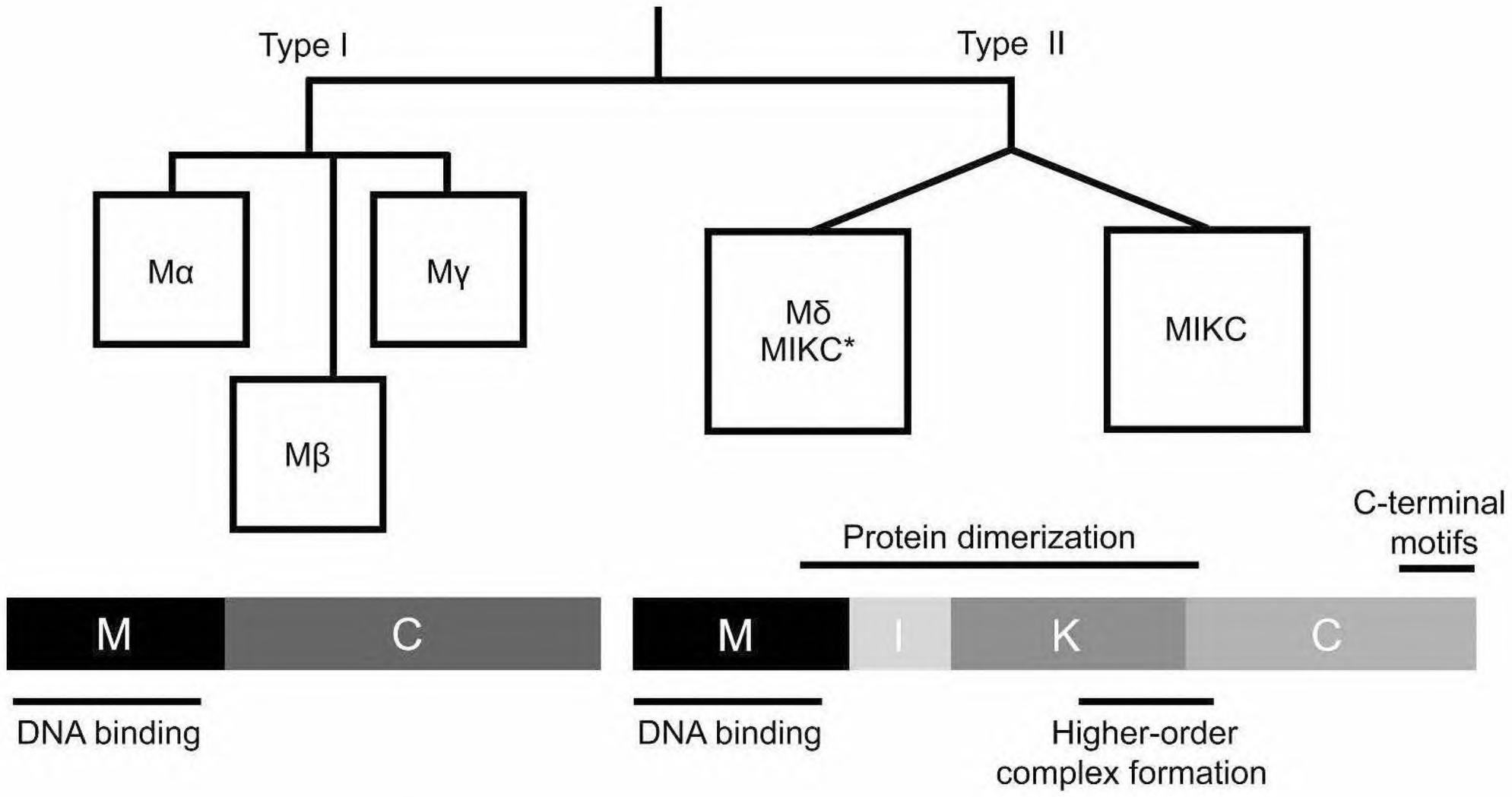


Figure 1. Schematic summary of the evolutionary relationships between the five major subfamilies of MADS-box containing loci. While all of the loci are defined by the presence of the MADS (M) domain, only the type II genes show conservation of three additional domains: Intervening (I), Keratin-like (K), and C-terminal (C). Note that the C-terminal region of the type I loci is completely distinct from that of the type II.

such as the core eudicot *Arabidopsis* (DC.) Heynh. and grass *Oryza* L. (reviewed in Zobell et al., 2010). Recently, MIKC* loci have been implicated in microgametophyte maturation and development, but much more work is required to understand whether this is a common feature of the subfamily (Adamczyk & Fernandez, 2009).

Although type I MADS-box genes outnumber type II in the *Arabidopsis* genome (Parenicova et al., 2003), their evolution and functions are comparatively poorly understood. The type I genes can be subdivided into the Mα, Mβ, and Mγ subfamilies, with Mβ being sister to Mγ (Fig. 1; Parenicova et al., 2003). They are much more diverse in their structures than the type II and lack a canonical K domain, although they do appear to form protein dimers (de Folter et al., 2005; Bemer et al., 2008). Two clear features have emerged regarding the type I MADS-box genes. First, they have experienced a much more rapid birth-and-death evolution than type II homologs (Nam et al., 2004). While phylogenetic analyses of type II loci result in many deeply conserved lineages, type I loci tend to cluster together by taxon, reflecting independent and relatively recent gene duplications (Nam et al., 2004; Arora et al., 2007). Second, they are commonly involved in the development of the female gametophyte and endosperm, as confirmed by both forward genetics and broad expression studies (Bemer et al., 2010b and references therein). These two features are possibly interrelated and may reflect the often rapid evolution of loci involved in fertilization processes (reviewed in Tian et al., 2009).

Since 2000, the development of high-throughput sequencing has facilitated transcriptome and genome analysis of a wide array of plant species, including *Arabidopsis*, *Oryza*, and *Vitis* L. (Joint Genome Institute, 2010). This work has facilitated evolutionary studies of gene lineage evolution across the angiosperms as well as comparative analysis of functional evolution within this context (e.g., Arora et al., 2007; Bowman et al., 2007). These studies have highlighted the critical interplay between gene duplication and functional divergence, even when primary sequence is highly conserved (e.g., Causier et al., 2005, 2010). To date, this work has primarily focused on the grass and core eudicot model systems, but new sequencing efforts now allow us to add a third major lineage of angiosperms in the form of the basal eudicot model *Aquilegia* L. (columbine) in Ranunculaceae. *Aquilegia* consists of ca. 70 perennial species distributed across temperate North America, Europe, and Asia (reviewed in Hodges & Arnold, 1994; Kramer, 2009). These recently diversified species have long fascinated researchers working in the fields of evolution and ecology due to their association of poor genetic differentiation with highly divergent pollinator syndromes (Hodges et al., 2004; Hodges & Derieg, 2009). More recently, *Aquilegia* has become a model for the evolution of floral morphology thanks to its novel floral organ types, which include first whorl petaloid sepals,

spurred petals in the second whorl, and a unique fifth organ type of sterile staminodia positioned between the fertile stamens and carpels (Kramer et al., 2007; Kramer, 2009). For all these reasons, as well as its relatively small genome size (~300 million basepairs [Mbp] 2C), *Aquilegia* is currently the subject of extensive genetic and genomic research that has produced an extensive expressed sequence tag (EST) dataset, a physical map, functional tools and, most recently, an 8X genome sequence produced by the Department of Energy (DOE) Joint Genome Institute (Kramer, 2009; Joint Genome Institute, 2010; Kramer & Hodges, 2010). This genome sequence comprises ca. 302 Mbp arranged in 971 scaffolds, of which ~2.9% is gap. In order to get a better understanding of the evolution of MADS-box genes and to create a resource for researchers interested in working with *Aquilegia*, we used the publically available first assembly of the hybrid *A. coerulea* E. James 'Origami' genome to identify MADS-box containing loci. The obtained sequences were used in phylogenetic analyses of the entire MADS-box family in order to assign subfamily affinities and were further included in more detailed studies of the MIKC^{C} subfamily to confirm lineage homology. These findings are discussed in the context of similar studies with particular consideration for the implications of deep patterns of MADS-box gene evolution.

Materials and Methods

Identification of MADS-box genes from the hybrid *Aquilegia coerulea* 'Origami' genome

In order to expand the set of 16 published *Aquilegia* MADS-box genes (Kramer et al., 2003, 2004, 2007), we used Basic Local Alignment Search Tool (BLAST) (Altschul et al., 1997) to perform a search of the recently released hybrid *A. coerulea* 'Origami' genome, annotation v1.0 (Joint Genome Institute, 2010) using previously identified MADS domain sequences from *Arabidopsis thaliana* (L.) Heynh., *Vitis vinifera* L., and *Oryza sativa* L. (Parenicova et al., 2003; Arora et al., 2007; Diaz-Riquelme et al., 2009). Specifically, we used the *Arabidopsis* sequences for *AGL16*, *AGL29*, *AGL33*, *AGL39*, *AGL48*, *AGL50*, *AGL58*, *AGL61*, *AGL80*, *AGL82*, *AGL86*, *AGL87*, *AGL97*, *AGL98*, *AGL100*, *AGL101*, *AGL103*, and *SEEDSTICK*; *Vitis* sequences for *VvAGL12*, *VvAGL17.1*, *VvFLC2*, and *VvTM8*; and *Oryza* sequences for *OsMADS62*, *OsMADS68*, *OsMADS89*, *OsMADS90*, *OsMADS94*, and *OsMADS96*. Each identified putative *Aquilegia coerulea* 'Origami' locus was examined for open reading frames using SoftBerry FGENESH (Salamov & Solovyev, 2000). Predicted protein and complementary DNA (cDNA) sequences were extracted and BLASTed back to both GenBank, in order to identify the MADS-box region and make initial assessments of affinity, and to the *Aquilegia* genome sequence itself to identify any other closely related paralogs. New MADS-box gene sequences were deposited in GenBank under accession numbers JX680222–JX680256 (Table 1).

Phylogenetic Analyses

Confirmed MADS-box containing loci were phylogenetically analyzed in order to determine their membership in the type I versus type II subfamilies. This required using ClustalW (Larkin et al., 2007) to construct an amino acid sequence alignment of the ~60 residue MADS domain. In addition to all of the *Aquilegia* sequences, this alignment included all *Arabidopsis* and *Oryza* MADS loci as well as *Vitis VvTM8* and *Solanum lycopersicum* L. *TM8* to represent the *TM8* lineage (see Arora et al., 2007; Diaz-Riquelme et al., 2009 for all accession numbers). Neighbor-joining (NJ) analysis was used on this dataset (Saitou & Nei, 1987) as implemented by PAUP* (Swofford, 2002). The NJ phylogeny (Fig. 2) was rooted along the branch separating the type II sequences (MIKC^{C} and MIKC*/Mδ) from those of type I, in keeping with previous studies (Alvarez-Buylla et al., 2000; Nam et al., 2004). The MIKC^{C} loci were further analyzed in order to determine specific affinities with deeply conserved lineages. This analysis used an amino acid alignment encompassing the M, I, and K domains (collectively termed MIK) of *Aquilegia*, *Arabidopsis*, *Oryza*, *Petunia* Juss., and *Vitis* MIKC^{C} representatives (for accession numbers see Table 1; Immink et al., 2003; Parenicova et al., 2003; Arora et al., 2007; Diaz-Riquelme et al., 2009). The completed alignment included 130 loci and 175 residues (contact author for alignments). Maximum likelihood (ML) phylogenetic analyses were performed using RAxML (Stamatakis et al., 2005; Stamatakis, 2014) as implemented by the CIPRES portal (Miller et al., 2009). For the purposes of the RAxML analyses, the best protein model of evolution was JTT (Jones) based on MrBayes 3.1 (Ronquist & Huelsenbeck, 2003; Huelsenbeck et al., 2008) amino acid mixed model tests (greater than 99 posterior probability [PP]). Branch support was estimated by performing 1000 replicates of fast bootstrapping (Stamatakis et al., 2008) using the same parameters as the original analysis. The *TM8* lineage was used to root this phylogeny, based both on the results of the analysis of the MADS domain alone and those of previous studies (Becker & Theissen, 2003). Matrixes and

Table 1. Hybrid *Aquilegia coerulea* E. James 'Origami' MADS-box genes with genome location. Expressed sequence tag (EST) numbers are for the Dana Farber Cancer Institute *A. formosa* Fisch. ex DC. × *A. pubescens* Coville database.

	Location					
Locus	Scaffold	MADS Pos	Strand	Type	EST	GenBank
AqAGL60	3	9581086	Plus	Alpha	none	JX680221
AqAGL61	82	280863	Minus	Alpha	none	JX680222
AqAGL62	31	2417989	Plus	Alpha	none	JX680223
AqAGL63	24	3291956	Minus	Alpha	none	JX680224
AqAGL64	96	478666	Plus	Alpha	none	JX680225
AqAGL65	2	5042310	Plus	Delta	TC33318	JX680226
AqAGL66	18	2220081	Minus	Alpha	none	JX680227
AqAGL67	18	3429116	Plus	Alpha	none	JX680228
AqAGL68	69	404345	Minus	Alpha	none	JX680229
AqAGL69	69	400144	Minus	Alpha	none	JX680230
AqAGL70	15	1987421	Plus	Alpha	none	JX680231
AqAGL71	52	729783	Plus	Alpha	none	JX680232
AqAGL72	41	479166	Plus	Alpha	none	JX680233
AqAGL73	7	190653	Minus	Alpha	none	JX680234
AqAGL74	5	5460796	Plus	Alpha	none	JX680235
AqAGL75	54	1514596	Plus	Alpha	none	JX680236
AqAGL80	1	4403062	Minus	Gamma	none	JX680237
AqAGL81	1529	2159	Minus	Gamma	none	JX680238
AqAGL82	112	22986	Plus	Gamma	none	JX680239
AqAGL83	29	109423	Minus	Gamma	none	JX680240
AqAGL84	7	5134489	Plus	Gamma	none	JX680241
AqAGL85	27	969516	Plus	Gamma	none	JX680242
AqAGL86	18	1770226	Minus	Beta/gamma	none	JX680243
AqAP3-1	6	2204058	Plus	MIKC	TC22599	EF489478
AqAP3-2	6	2147564	Plus	MIKC	TC24405	EF489477
AqAP3-3	7	3032344	Plus	MIKC	TC20315	EF489476
AqAP3-3b	38	1797328	Plus	MIKC	none*	HQ694798
AqPI	14	1712364	Minus	MIKC	TC21654	EF489475
AqBS	22	2313113	Minus	MIKC	none*	AY436713
AqSEP1	6	8363818	Minus	MIKC	TC30455	JX680244
AqSEP2A	2	6945234	Minus	MIKC	TC23935	JX680245
AqSEP2B	2	6911967	Minus	MIKC	none	JX680246
AqSEP3	11	2306215	Plus	MIKC	TC20920	JX680247
AqAGL6	13	3100284	Minus	MIKC	TC27019	JX680248
AqAGL17	10	436736	Minus	MIKC	none	JX680249
AqAGL12	14	490009	Plus	MIKC	none	JX680251
AqAGL15	9	1871509	Minus	MIKC	TC30235	JX680250
AqAG1	136	79379	Minus	MIKC	TC22246	AY464111
AqAG2	22	731674	Plus	MIKC	none*	AY464110
AqAGL24.1	15	1246754	Minus	MIKC	TC24816	HQ173338
AqAGL24.2	7	4643609	Plus	MIKC	TC33172**	HQ173339
AqFL1A	2	6930012	Minus	MIKC	TC23520	JX680252
AqFL1B	2	6899144	Minus	MIKC	TC27021	JX680253
AqSOC1.1	13	3057695	Plus	MIKC	DR913118	HQ173336
AqSOC1.2	35	2391819	Minus	MIKC	TC31575	JX680254
AqSOC1.3	3	9953490	Plus	MIKC	none	JX680255
AqSOC1.4	5	8820680	Minus	MIKC	none	JX680256

* Locus is not represented in the EST database, but expression has been confirmed using reverse transcriptase (RT)-polymerase chain reaction (PCR).

** EST is incorrectly spliced.

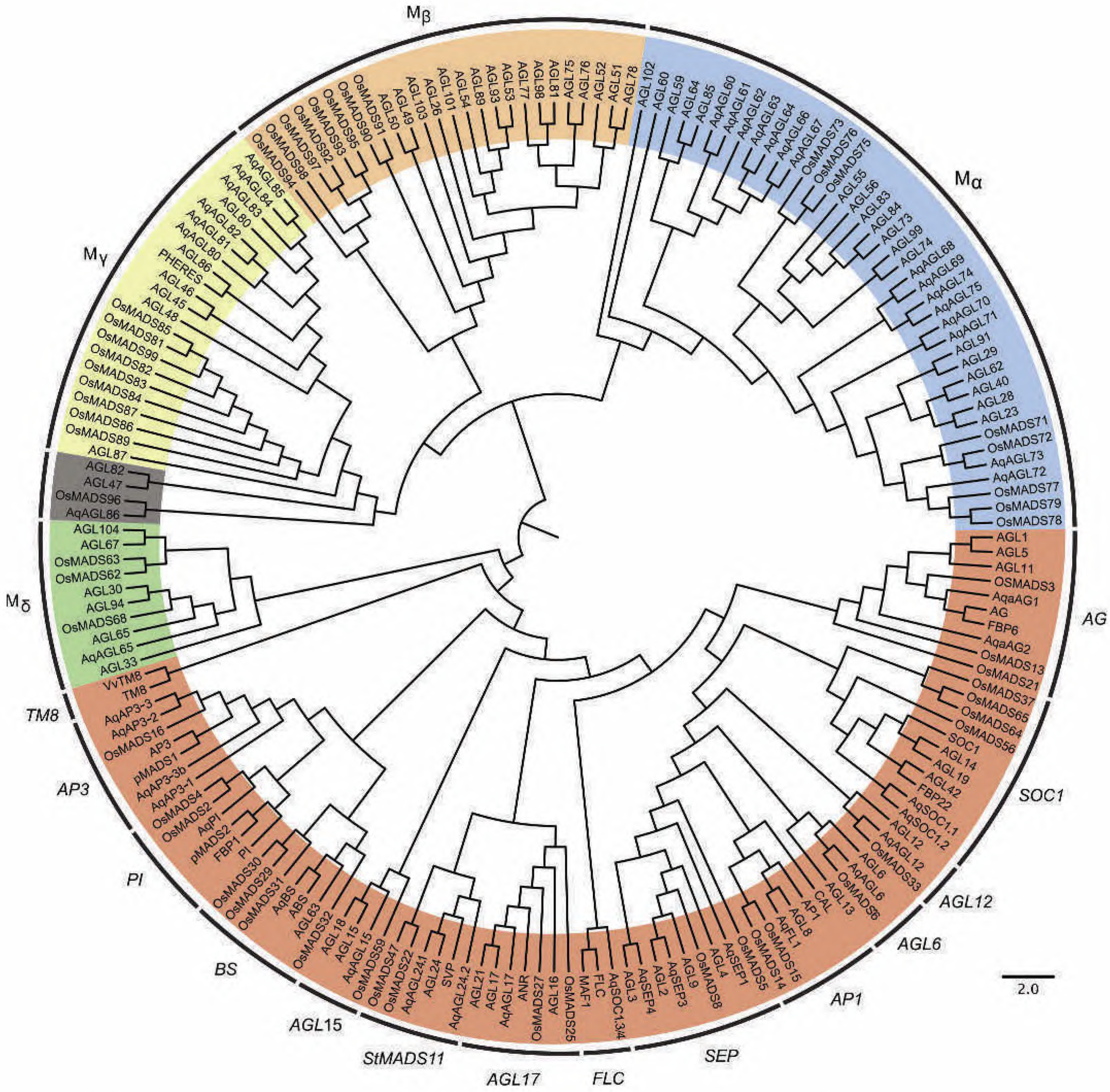


Figure 2. Neighbor-joining (NJ) analysis of MADS domain sequences from all identified *Aquilegia*, *Arabidopsis*, and *Oryza* loci. Specific lineages are indicated by colors and bracketing. The type I lineages are the Mγ (yellow), Mβ (orange), and Mα (blue), while the type II are the MIKC^{C} (red, with individual lineages denoted by brackets) and MIKC* (or Mδ; green). A paraphyletic group of four loci are colored in gray. In addition to the new *AqAGL86* sequence, these include three sequences (*AGL47*, *AGL82*, and *OsMADS86*) that have previously been placed with Mβ but are instead associated with Mγ in our analysis.

trees associated with this study were deposited in TreeBase (<http://purl.org/phylo/treebase/phylows/study/TB2:S13212>).

Results and Discussion

The MADS-box family of the hybrid *Aquilegia coerulea* 'Origami'

We have identified 47 MADS domain containing loci in the recently sequenced genome of the hybrid *Aquilegia coerulea* 'Origami' (Table 1; Fig. 2). These genes are distributed across 29 different scaffolds that range in size from almost 2 Mbps to 355 kilo basepaird (Kbps). Scaffolds 2, 3, 4, 6, 7, 13, 14, 15, 18, 22, and 69 contain multiple MADS-box loci, but only scaffolds 2, 18, and 69 appear to represent tandem duplications (see below for further discussion). Note that we detected two scaffolds that appear to have assembly errors: 136, which has two identical tandem copies of *AqAG1*, and 96, which has two identical tandem copies of *AqAGL64*. These duplicates, which we believe to be artificial, were not included in the analysis.

An NJ analysis of all of the recovered MADS domains demonstrates that 23 loci distributed across 18 scaffolds fall into type I, while 24 loci distributed across 15 scaffolds are placed in type II. Overall, the phylogenetic tree typology of MADS domain se-

quences from all identified *Arabidopsis*, *Aquilegia*, and *Oryza* loci (Fig. 2) is largely consistent with previous studies (Parenicova et al., 2003; Arora et al., 2007). The one inconsistency is the placement of *AGL47*, *AGL82*, and *OsMADS96* relative to the Mβ and Mγ subfamilies, which will be further discussed below. The total number of MADS domain loci identified, 47, is considerably less than the 107 and 75 known from *Arabidopsis* and *Oryza*, respectively (Parenicova et al., 2003; Arora et al., 2007). This is likely due to two factors. First, both *Arabidopsis* and *Oryza* have experienced genome duplication events in their relatively recent genomic history (De Bodt et al., 2005), which may have increased the numbers of MADS-box loci. Second, this study was conducted using the v1.0 annotation of the hybrid *Aquilegia coerulea* 'Origami' genome, meaning that further annotation may yet identify additional loci.

TYPE I MADS-BOX GENES

The *Aquilegia* type I clade contains three monophyletic lineages roughly corresponding to the previously defined Mα, Mβ, and Mγ (Fig. 2). The Mα clade includes 15 *Aquilegia* representatives, which appear to define at least three separate lineages that are largely independently diversified relative to the *Arabidopsis* and *Oryza* representatives. The Mγ clade contains six *Aquilegia* representatives that are, again, likely to be independently radiated from the other identified loci. The one point of disagreement between our analysis and previous studies is the placement of the *Arabidopsis* sequences *AGL47* and *AGL82* and the *Oryza OsMADS96*. Parenicova et al. (2003) placed *AGL47* and *AGL82* in the Mβ clade, albeit with no support. Likewise, the analysis of Arora et al. (2007) identified *OsMADS96* as an Mβ representative but with no reported support. In our analysis, these three loci fall out with a new *Aquilegia* sequence, *AqAGL86*, as paraphyletic to the Mγ clade rather than with the Mβ. Closer inspection of the four complete sequences reveals no obvious shared motifs, either among *AGL47/82*, *OsMADS96*, and *AqAGL86* or between these genes and either the Mβ or Mγ homologs (Parenicova et al., 2003; Arora et al., 2007; and data not shown). Given that our analysis similarly lacks support for these relationships, we cannot make strong conclusions beyond saying that *AqAGL86* is currently associated with the Mγ clade.

This raises the larger question, however, of how conserved the Mβ lineage really is across angiosperms. Previous studies held that Mβ representatives were specific to the Brassicaceae (Leseberg et al., 2006), but Arora et al. (2007) recovered an apparent clade of *Oryza* Mβ loci. Likewise, in our NJ analysis, most of these same *Oryza* genes are associated with the original Mβ genes from *Arabidopsis* (Fig. 2). It is interesting to note, however, that no clear Mβ representatives have been recovered from the *Aquilegia* genome yet. Furthermore, examination of the putative Mβ *Arabidopsis* and *Oryza* loci does not reveal any obvious shared motifs, either within the MADS domain or outside it (Parenicova et al., 2003; Arora et al., 2007). Given this rather weak association between the *Arabidopsis* and *Oryza* Mβ loci, along with their apparent absence from the *Aquilegia* genome, it may be necessary to re-examine the question of whether the Mβ lineage is truly conserved across the angiosperms. Of course, the annotation of the *Aquilegia* genome is in its early stages, and Mβ loci may yet be discovered.

In terms of patterns of genomic structure, most of the type I genes are relatively dispersed across different scaffolds. There are three pairs—*AqAGL66/67*, *AqAGL68/69*, and *AqAGL84/85*—that represent interesting cases. Each one of these pairs has identical or almost identical MADS domain sequences, while the rest of the coding regions contain a small number of clear differences. Thus, we have annotated them as separate loci, but it is likely that they are derived from relatively recent duplication events. One of the pairs, *AqAGL68/69*, is in fact close together on the same scaffold (69), suggesting a recent tandem duplication. However, the other two pairs are not close together, with *AqAGL66/67* on the same scaffold (18) but 1.2 Mbp apart and *AqAGL84/85* on completely different scaffolds (7 and 27). Although it is possible that scaffolds 7 and 27 will ultimately be joined into one chromosomal unit, these scaffolds are approximately 6.1 and 3 Mbp, respectively, so the loci are at least 2 Mbp apart based on their locations in the scaffolds. Neither of these pairs shows evidence of shared synteny that would suggest a large-scale duplication event. As is typical for type I loci (De Bodt et al., 2003), the *Aquilegia* representatives are predicted to contain few if any introns, with only four loci predicted to have either one (*AqAGL60*, *AqAGL63*, *AqAGL69*) or two (*AqAGL73*) introns. It is interesting to note in this regard that for the apparent tandem duplication pair *AqAGL68/69*, the former lacks introns while the latter has one, possibly reflecting a retroduplication origin for *AqAGL68*.

TYPE II MADS-BOX GENES

Of the 24 type II MADS-box genes, only one member is in the MIKC* subfamily, *AqAGL65*, a homolog of the P-clade (Nam et al., 2004), with the balance in the MIKC^{C}. Many of the *Aquilegia* MIKC^{C}

members have been previously described, particularly in regard to their potential roles in novel floral organ identity in *Aquilegia* (Kramer et al., 2003, 2004, 2007; Sharma et al., 2011), but this is the first report for six of the loci (*AqAGL12*, *AqAGL15*, *AqAGL17*, *AqSOC1.2*, *AqSOC1.3*, *AqSOC1.4*). Of these new loci, *AqAGL15* and *AqSOC1.2* are also represented by ESTs in the *A. formosa* Fisch. ex DC. × *A. pubescens* Coville databases, but expression of the remaining loci has not yet been demonstrated (Table 1). There is one previously published locus, *AqFL2*, which was originally isolated from *A. vulgaris* L., but we have been unable to identify it in the hybrid *A. coerulea* 'Origami' genome. A partial coding region for *AqFL2* was defined based on four identical cDNA fragments that were obtained in the process of cloning the full-length *AqFL1* cDNA. Given that *AqFL2* appears to be a representative of an ancient paralogous *FUL*-like lineage in the Ranunculales (Litt & Irish, 2003), we are inclined to believe that it was not a spurious identification, but the possibility exists that it has either been lost from the hybrid *A. coerulea* 'Origami' genome or has not been covered by current sequencing. *AqSOC1.3/AqSOC1.4* are also of particular note since they lack introns and, thus, appear to be retroduplications. The two open reading frames are almost identical but are located on different scaffolds (3 and 5, respectively) with different neighboring loci, including predicted transposon sequence flanking *AqSOC1.4*, which further supports the retroduplication hypothesis. Although *AqSOC1.3/AqSOC1.4* are associated with *FLC* in the MADS domain analysis (Fig. 2), this is not supported by the MIK analysis (see below). Another interesting point is that *AqFL1* and *AqSEP2* are each represented twice in the genome, being part of a large segmental duplication on scaffold 2. We term these loci *AqFL1A/B* and *AqSEP2A/B*. Both homeologous pairs contain introns of different lengths but have only a very small number of differences in their coding regions. It appears that ESTs from three of the four loci are present in the *A. formosa* × *A. pubescens* database (Table 1), with *AqSEP2B* remaining to be confirmed as an expressed locus.

In order to better understand the phylogenetic relationships among *Aquilegia* MIKC^{C} loci, we created an amino acid alignment covering the MIK domains, which can be confidently aligned across the entire subfamily. We expanded sampling in this dataset to include *Petunia* and *Vitis* homologs and analyzed it using ML as implemented by RAxML software (Fig. 3). The topology of the resultant phylogeny is largely consistent with previous studies (Becker & Theissen, 2003; Gramzow & Theissen, 2010). Although *AqSOC1.3/AqSOC1.4* are associated with the *FLC* lineage (Fig. 2), they fall into the *SOC1* clade with strong support in the MIK analysis (Fig. 3A). This reflects the fact that while *AqSOC1.3/AqSOC1.4* have rather divergent MADS domains, their I-, K-, and C-terminal domains contain synapomorphic motifs for the *SOC1* subfamily. Unlike *AqSOC1.3/AqSOC1.4*, the other subfamily members, *AqSOC1.1/AqSOC1.2* have the typical six introns associated with MIKC^{C} loci. Therefore, no *Aquilegia* representatives have been identified for the *FLC* or *TM8* lineages, highlighting the mysterious nature of both. *FLC* is notable because although it is a highly pleiotropic locus in *Arabidopsis*, affecting vernalization response, temperature-dependent germination, water use, and phase change (McKay et al., 2003; Alexandre & Hennig, 2008; Chiang et al., 2009; Willmann & Poethig, 2011), orthologs have yet to be identified outside the core eudicots (Becker & Theissen, 2003; Gramzow & Theissen, 2010). Despite some possible evidence for a conserved role in flowering time response (Reeves et al., 2007), no direct functional data exist for *FLC* orthologs in other core eudicots, and the source of their derivation remains unclear. One possibility is that the lineage was derived from the γ hexaploidization event at the base of the core eudicots (Jiao et al., 2012; Vekemans et al., 2012), but even if that is the case, it remains to be determined what the most closely related lineages might be and which aspects of the complex functional repertoire in *Arabidopsis* might be conserved across core eudicots. The *TM8* lineage is even more enigmatic. Very few homologs have been identified, the majority of which are found in the core eudicots (although *Arabidopsis* lacks a *TM8* ortholog; Becker & Theissen, 2003), and no function has yet been ascribed to any member. The ongoing, extensive transcriptomic and genomic studies of diverse angiosperms will hopefully help answer some of these questions.

Conclusion

Aquilegia is an important new model system for the study of both ancient and recent evolutionary processes. Our identification of a large number of MADS-box containing loci will aid comparative studies seeking to bridge the gap between grass and core eudicot models. In particular, the characterization of a large number of type I MADS-box genes will allow researchers to determine whether the novel expression patterns and functions associated with these loci are deeply conserved across the angiosperms. Overall, our finding that the *Aquilegia* type I and type II subfamilies have very different evolu-

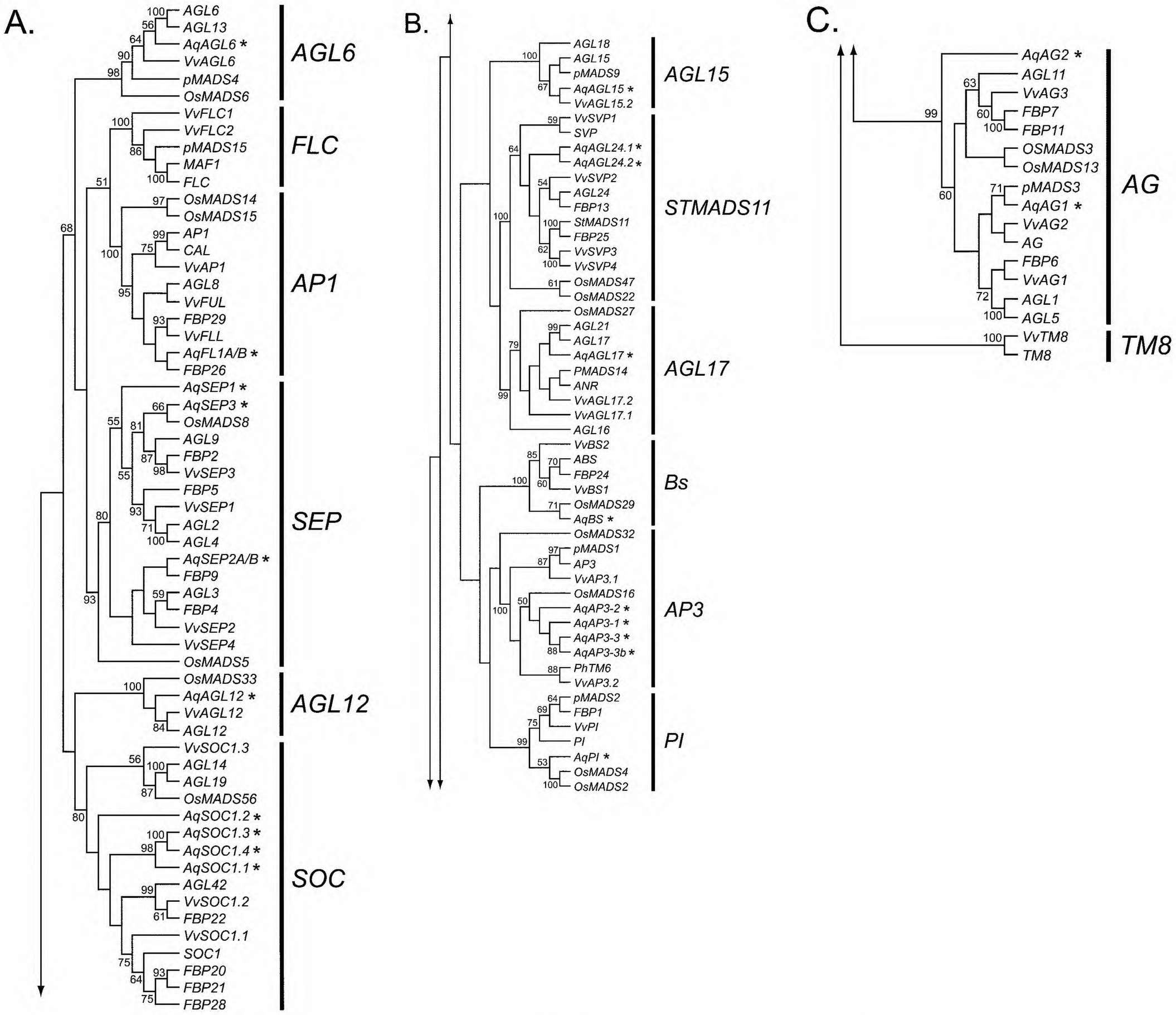


Figure 3. Maximum Likelihood (ML) analysis of the MIK domain sequences from *Aquilegia*, *Arabidopsis*, *Oryza*, *Petunia*, and *Vitis*, and MIKC^{C} loci. Bootstrap support values of more than 50% are indicated at nodes. Brackets on the right denote specific lineage affiliations. Asterisks indicate *Aquilegia* loci.

tionary histories is consistent with similar studies in *Arabidopsis*, *Petunia*, and *Oryza* (Immink et al., 2003; Parenicova et al., 2003; Arora et al., 2007). On the other hand, although there are some examples of seemingly recent gene duplication events across these loci, there appear to be fewer tandem paralogs, especially among the type I loci, than has been observed in other models (De Bodt et al., 2003; Nam et al., 2004; Bemer et al., 2010a). This seems to be consistent with an overall smaller number of MADS-box genes in *Aquilegia*.

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EVOLUTION AND DEVELOPMENT OF TENDRILS IN BIGNONIEAE (LAMIALES, BIGNONIACEAE)[1]

Mariane S. Sousa-Baena,[2,3] *Neelima Roy Sinha,*[3] *and Lúcia G. Lohmann*[2]

ABSTRACT

The tribe Bignonieae includes all Neotropical lianescent Bignoniaceae. The leaves of Bignonieae are generally 2- or 3-foliolate, with terminal leaflets modified into a tendril. These tendrils have varied morphologies and are thought to have been involved in the diversification of Bignonieae. Little, however, is still known about the biology and evolution of tendrils. This study investigated the evolution and development of tendril types in Bignonieae in order to further understand how changes in leaf morphogenesis led to current patterns of variation in tendril morphology. For that, we investigated the ontogeny of 11 species representing a wide diversity of tendril types (i.e., simple, trifid, and multifid) and used a recently published phylogeny of Bignonieae as the basis to reconstruct patterns of evolution for tendril types. For those analyses, we used maximum likelihood (ML) and maximum parsimony (MP) approaches, with both ACCTRAN and DELTRAN optimization schemes implemented in the latter. Ancestral character state reconstructions of tendril type suggest that the ancestral condition for the whole tribe (Core Bignonieae plus *Perianthomega* Bureau ex Baill.) is a lack of tendrils, whereas parsimony reconstructions indicate an ambiguous ancestral condition. However, all reconstructions suggest that trifid tendrils represent the ancestral condition for the Core Bignonieae. Other tendril types evolved subsequently through a series of developmental changes. Furthermore, tendril ontogenetic studies provided key information for the resolution of major ambiguities in the ancestral state reconstructions of tendril type in Bignonieae. For instance, in *Bignonia callistegioides* Cham. and *B. prieurei* DC. (simple tendrils), no traces of remnant lateral branches from a trifid-tendrilled ancestor were found, corroborating the ACCTRAN hypothesis of a simple tendril condition for the ancestor of that lineage. In *Tanaecium pyramidatum* (Rich.) L. G. Lohmann (trifid tendrils), on the other hand, we detected a pattern and rate of tendril differentiation that initially followed the same pattern seen in taxa with simple tendrils (i.e., *Cuspidaria* DC. and *Fridericia* Mart.), with a developmental delay relative to other trifid-tendrilled species, favoring a simple-tendrilled ancestor hypothesis and supporting the ML and ACCTRAN optimizations. The interpretation of the ontogenetic data in light of a robust phylogenetic framework led to specific hypotheses about the evolutionary processes and respective changes in gene regulation that may have led to the current tendril morphologies found in Bignonieae. In particular, we suggest that tendril evolution involved heterochrony and hypothesize that changes in the expression of genes that are associated with compound leaf development may have led to the diversity of tendril morphology currently observed in Bignonieae.

Key words: Ancestral character state reconstructions, Bignoniaceae, Bignonieae, compound leaves, development, evolution, heterochrony, lianas, tendrils.

Lianas account for a large percentage of the leaf biomass and floristic diversity in tropical forests (Gentry, 1991; Schnitzer, 2005), contribute ca. 44% of the woody species in some regions of the Amazon Rainforest (Pérez-Salicrup, 2001), and are important for the dynamics of forest structure and composition (Schnitzer & Bongers, 2002; Isnard & Silk, 2009). The abundance and density of lianas rise considerably with forest disturbance (Schnitzer & Bongers, 2002; Bradshaw et al., 2009), which has led to a recent increase in the interest in liana research (van der Heijden et al., 2010; Zhu & Cao, 2010; Gallagher & Leishman, 2012; Garbin et al., 2012).

The lianoid habit and associated structural modifications have intrigued biologists since Darwin (1875). Considerable research has been conducted on the stem anatomy of lianas, which include an unusual pattern of cambium activity, resulting, for

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instance, in a xylem furrowed by phloem wedges, as observed in Bignonieae, or in the development of multiple steles, as seen in Sapindaceae (Dobbins, 1971; Dobbins & Fisher, 1986; Carlquist, 1988; Gasson & Dobbins, 1991; Gabrielli, 1993; Pace et al., 2009).

Tendrils represent another key feature associated with the evolution of the climbing habit (Gentry, 1980). Tendrils are filiform organs that have the ability to twine around other structures, representing an efficient climbing strategy (Darwin, 1875). They are defined by their function and can have different ontogenetic origins, representing the modification of leaves, leaflets, stipules, branches, inflorescences, or even roots (Putz & Holbrook, 1991). More specifically, leaf tendrils evolved several times during the evolutionary history of the angiosperms (Gentry, 1980), in particular, in families such as Colchicaceae (Liliales; Nordenstam, 1998), Polemoniaceae (Ericales; Wilken, 2004), Ranunculaceae (Ranunculales; Tamura, 1993), Papaveraceae (Ranunculales; Kadereit, 1993), Asteraceae (Asterales; Hind, 2007), Lophopyxidaceae (Malpighiales; Takhtajan, 1997), Dioncophyllaceae (Caryophyllales; Takhtajan, 1997), Fabaceae (Fabales; Darwin, 1875), and Bignoniaceae (Lamiales; Fischer et al., 2004). Interestingly, although all of these families have evolved foliar modifications to climb, such modifications are morphologically different and not homologous. However, leaf tendril types present in these distantly related plant families share an interesting characteristic: they are apparently radial structures originated from an organ with dorsoventral polarity (leaves). For instance, in the Polemoniaceae tendrils are modified leaflets (Wilken, 2004), in the Colchicaceae tendrils are leaf tips that are adapted to climb (cirrhose leaf apex; Nordenstam, 1998), and in the Dioncophyllaceae tendrils are the tips of the leaf midribs that become forked and develop a pair of hooks (Takhtajan, 1997). Despite the morphological diversity and ecological importance of leaf tendrils, very little is still known about their evolution and development outside Fabaceae, in which multiple taxa have been studied (Champagne et al., 2007; Hofer et al., 2009).

The morphology of leaf tendrils is especially diverse in Bignonieae (Bignoniaceae), which includes ca. 400 species (Lohmann & Ulloa, 2006 onwards) and represents the largest clades of Neotropical lianas (Gentry, 1991; Spangler & Olmstead, 1999; Lohmann, 2006; Olmstead et al., 2009). In Bignonieae, most tendrils arise by modifications of the terminal leaflets of the 1- to 3-ternate leaves, with the exception of *Perianthomega vellozoi* Bureau, which climbs exclusively with the aid of twinning petioles (Lohmann, 2006; Lohmann & Taylor, 2014). Tendrils across Bignonieae exhibit remarkable morphological diversity, varying from simple to bifid, trifid, or multifid, with some species possessing adhesive discs or hooks at the tip (cf. Fig. 1; Lohmann, 2006; Lohmann & Taylor, 2014). Foliar tendrils also occur in the Tourrettieae, a tribe that is restricted to the Andes and includes four species with branched foliar tendrils (Gentry, 1980; D'Arcy, 1997; Olmstead et al., 2009). Tendrils are lacking in the Paleotropical Bignoniaceae, a phenomenon thought to be associated with the lower speciation rates of the lianoid Bignoniaceae in the Old World (Gentry, 1991). In contrast, the acquisition of tendrils in the Neotropics may represent a key innovation that led to the incredible diversification of liana Bignoniaceae in that region (Gentry, 1991).

Although simple in structure, tendrils undergo complex modifications during development that result from negative phototropism, circumnutation, thigmotropism, and contact coiling (Darwin, 1875; Jaffe & Galston, 1968; Jaffe et al., 2002; Monshausen et al., 2008). During coiling, tendrils display an increase in respiration rate after contacting a support (Riehl & Jaffe, 1982). Furthermore, modifications in membrane permeability are coupled with an increase in solute efflux (Jaffe & Galston, 1968; Jaffe, 1975; Liss & Weiler, 1994; Engelberth, 2003). The appearance of cortical gelatinous fibers is also associated with tendril coiling in several plant species (Meloche et al., 2007; Bowling & Vaughn, 2009). All of these processes are coordinated by an intricate hormonal regulation (Junker, 1976; DeMason & Chawla, 2004) and are responsible for tendril development in the angiosperms.

Most developmental studies involving foliar tendrils were conducted on peas (*Pisum sativum* L.) and other species that belong to the inverted repeat-lacking clade (IRLC) of legumes (Gourlay et al., 2000; Champagne et al., 2007; Hofer et al., 2009). This clade also includes *Vicia* L., *Lathyrus* L., and *Lens* Mill., all of which bear foliar tendrils (Wojciechowski et al., 2004). Pea leaves are compound, comprised of a basal pair of stipules, one or more pairs of opposite leaflets, and a terminal branched tendril. Pea leaf primordia develop acropetally, with the tendril identity of the terminal leaflet primordium only being determined at the fourth plastochron (Gould et al., 1994).

Significant progress has been made toward a better understanding of the molecular mechanisms that regulate pea leaf development. While class 1 *KNOTTED1*-like (*KNOX1*) genes appear to control

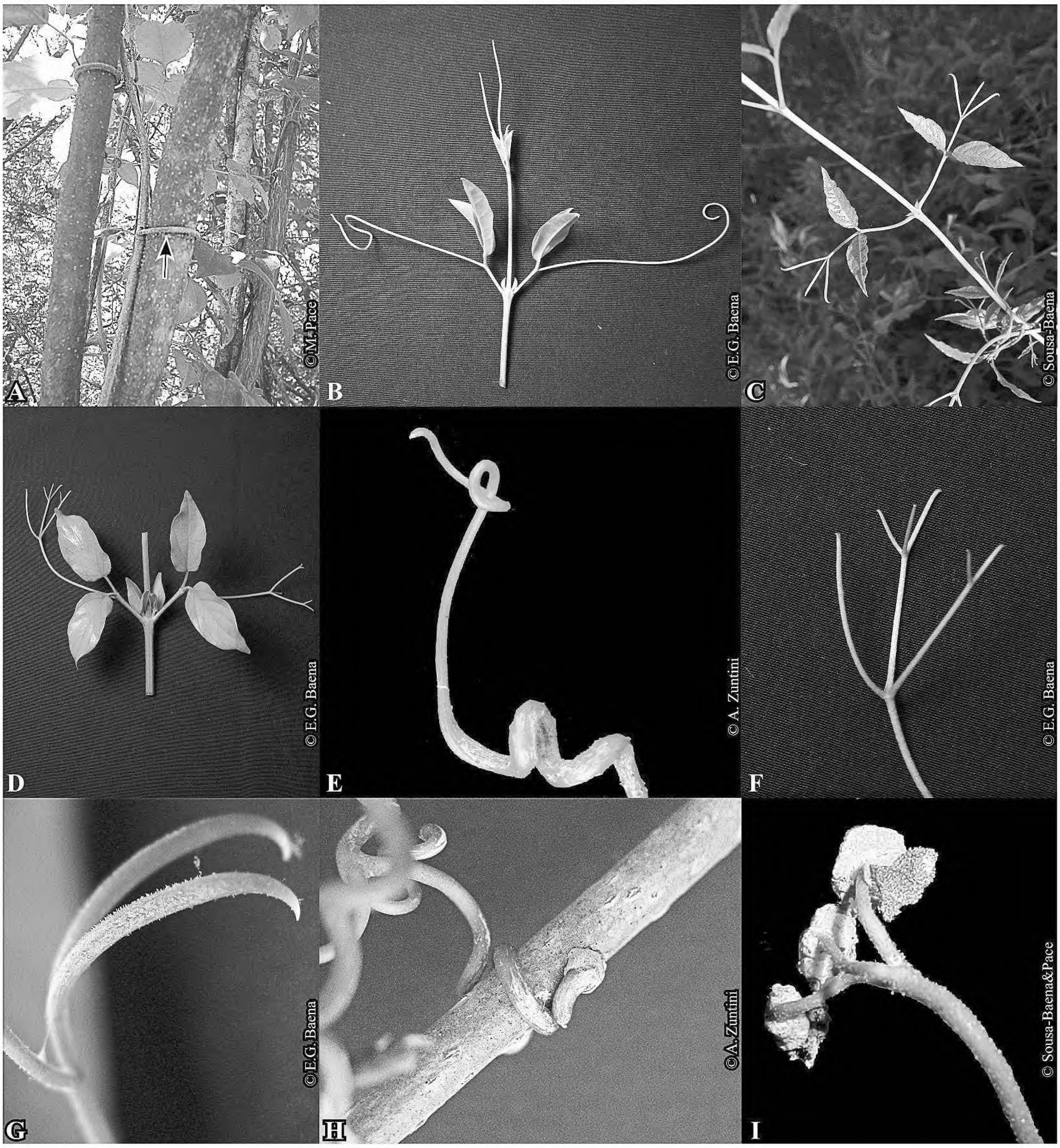


Figure 1. Sample of climbing organs found in Bignonieae. —A. *Perianthomega vellozoi* (*Pace 10*, SPF), twinning petiole (arrow). —B. *Bignonia callistegioides* (*Sousa-Baena 3*, DAV), opposite leaves composed of two leaflets and a terminal simple tendril. —C. *Dolichandra unguis-cati* (*Groppo 322*, SPF), compound leaves with a terminal trifid tendril. —D. *Amphilophium buccinatorium* (*Sousa-Baena 4*, DAV), compound leaves with a terminal multifid tendril. —E. *Adenocalymma bracteatum* (Cham.) DC. (*Lohmann 861*, SPF), detail of a simple tendril. —F. *Amphilophium buccinatorium*, detail of a multifid tendril. —G. *Dolichandra unguis-cati*, detail of a trifid tendril showing the uncinate tips. —H. *Amphilophium crucigerum* (*Pace 1*, SPF), tendril tip with adhesive disc. —I. *Tynanthus cognatus* (Cham.) Miers (*Pace 9a*, SPF), detail of a trifid tendril tip showing the adhesive discs.

the development of compound leaves across angiosperms (Sinha, 1999; Champagne & Sinha, 2004), *UNIFOLIOLATA*, a *LEAFY/FLORICAULA* ortholog, seems to regulate compound leaf development in peas (Hofer & Ellis, 1998; Champagne & Sinha, 2004). Recent studies on the garden pea (*Pisum* L.) and on the sweet pea (*Lathyrus*) indicated that the expression of *TENDRILLESS*, positively regulated by *UNIFOLIOLATA/LEAFY*, in the terminal pinnas of the wild leaf prevents leaflets from developing into a blade, leading to the formation of tendrils instead (Hofer et al., 2009).

Despite recent advances in molecular genetics of tendrils in model organisms, very little is still known

Table 1. Species sampled in the ontogenetic study, followed by their respective tendril type and phylogenetic placement. For species with polymorphic tendril types, the most common state is indicated first in the column.

Species	Tendril type	Phylogenetic placement
Bignonia prieurei DC.	simple	clade with ambiguous ancestral tendril type
B. callistegioides Cham.	simple	clade with ambiguous ancestral tendril type
Cuspidaria convoluta (Vell.) A. H. Gentry	simple	clade with a simple-tendrilled ancestor
Fridericia conjugata (Vell.) L. G. Lohmann	simple	clade with a simple-tendrilled ancestor
F. samydoides (Cham.) L. G. Lohmann	simple	clade with a simple-tendrilled ancestor
F. speciosa Mart.	simple	clade with a simple-tendrilled ancestor
Tanaecium pyramidatum (Rich.) L. G. Lohmann	bifid/trifid	clade with ambiguous ancestral tendril type
Dolichandra unguis-cati (L.) L. G. Lohmann	trifid	clade with a trifid-tendrilled ancestor
Mansoa difficilis (Cham.) Bureau & K. Schum	trifid	clade with a trifid-tendrilled ancestor
Amphilophium crucigerum (L.) L. G. Lohmann	trifid/multifid	clade with a trifid-tendrilled ancestor
Amphilophium buccinatorium (DC.) L. G. Lohmann	trifid/multifid	clade with a trifid-tendrilled ancestor

about the anatomy, morphogenesis, or evolution of tendrils in nonmodel organisms. The great diversity in tendril morphology encountered in representatives of Bignonieae, coupled with the availability of a robust phylogeny for the group (Lohmann, 2006), makes the tribe very suitable for investigating the evolution and development of tendrils.

Herein, we study the development of different tendril types in various representatives of Bignonieae and investigate the patterns of ontogenetic change within an evolutionary framework. We evaluate the historical order of change in morpho-anatomical features associated with tendrils, and suggest potential evolutionary processes that may have led to the diversity of tendrils currently encountered in the tribe. We further relate our findings to genes that are known to regulate leaf development in angiosperms, and discuss the potential role of those genes for the evolution of tendrils in Bignonieae.

Materials and Methods

Ancestral character state reconstructions

Phylogeny

We used the single tree that resulted from the maximum likelihood (ML) analysis of a combined molecular dataset (*PepC* + *ndhF*; Lohmann, 2006) as a framework in which to map the ancestral character states of the character tendril type and estimate the historical order of appearance of the various tendril types in Bignonieae. This tree included 104 terminals of Bignonieae for which *ndhF* and *PepC* sequences were available for all taxa, plus *Perianthomega vellozoi* for which only *ndhF* sequences were available. This additional species was included in the analysis with *PepC* characters coded as missing data.

Character coding

Coding of the character "tendril type" was extracted from the morphological matrix of Lohmann (2003) and Lohmann et al. (in prep.), which included the exact same 104 terminals as the combined molecular phylogeny (Lohmann, 2006). The character tendril type was coded as "absent" when terminal leaflets modified in tendrils were lacking, as "simple" when the apices of tendrils were not parted, as "bifid" when parted twice, as "trifid" when parted three times, and as "multifid" when parted multiple times. Character coding was based on herbarium specimens that represented young and adult individuals collected in several localities. In Bignonieae, tendril type morphology is generally fixed within a species and not correlated with environmental conditions. Even though *Perianthomega vellozoi* bears simple tendrils, the tendrils of this species are twinning petioles rather than modified leaflets and so, tendrils were coded as absent in this species. The character tendril type and its respective character states were coded as discrete, non-overlapping, and multistate (for further details, see Lohmann, 2003; Lohmann et al., in prep.). When species had polymorphic tendril types (*Tanaecium pyramidatum* (Rich.) L. G. Lohmann, *Amphilophium crucigerum* (L.) L. G. Lohmann, and *A. buccinatorium* (DC.) L. G. Lohmann; Table 1), our coding used the majority rule criterion of Wiens (1999), and the most common character state was used.

Ancestral character state reconstructions

Reconstructions of the character tendril type were conducted under maximum parsimony (MP) (Maddison & Maddison, 1992) and ML assumptions (Maddison & Maddison, 2009), with tendril type treated as unordered and unweighted. Parsimony

reconstructions used the all-most-parsimonious states trace option, and implemented the accelerated (ACCTRAN) and delayed (DELTRAN) trace options (Maddison & Maddison, 1992).

ONTOGENETIC STUDIES

Taxon sampling

We selected 11 species representing seven different genera (i.e., *Amphilophium* Kunth, *Bignonia* L., *Cuspidaria* DC., *Dolichandra* Cham., *Fridericia* Mart., *Mansoa* DC., and *Tanaecium* Sw.) that included a wide diversity of tendril morphologies and whose developmental data had greater potential to clarify ambiguities in tendril ancestral character state reconstructions for the ontogenetic studies (Table 1). This sampling scheme was intended to cover the breadth of variation in tendril morphology encountered in Bignonieae, as well as to help resolve ambiguities in the ancestral character state reconstructions. Specifically, we sampled six species with simple tendrils (*B. prieurei* DC., *B. callistegioides* Cham., *C. convoluta* (Vell.) A. H. Gentry, *F. conjugata* (Vell.) L. G. Lohmann, *F. samydoides* (Cham.) L. G. Lohmann, and *F. speciosa* Mart.), four species with trifid tendrils (*A. crucigerum*, *D. unguis-cati* (L.) L. G. Lohmann, *M. difficilis* (Cham.) Bureau & K. Schum., and *T. pyramidatum*), and one species with multifid tendrils (*A. buccinatorium*). Apart from representing a wide diversity of tendril types, these taxa were selected to include representatives of clades with well-established tendril conditions (i.e., homogeneous lineages in terms of tendril morphology and whose ancestral tendril condition was clear) as well as representatives of clades with ambiguous ancestral tendril types. Samples from clades with well-defined ancestors were intended to characterize the typical pattern of development for each tendril type. On the other hand, sampling of species from clades with ambiguous ancestral tendril reconstructions aimed at contributing further data toward the resolution of these ambiguities.

We used the phylogeny of Bignonieae (Lohmann, 2006), with the character tendril type mapped onto it (Fig. 2), as a basis to select taxa for the ontogenetic study. Overall, we sampled four species belonging to two genera with well-established simple tendrils (*Cuspidaria* and *Fridericia*), and three species belonging to three genera with well-established trifid tendrils (*Amphilophium*, *Dolichandra*, and *Mansoa*). In addition, we sampled representatives from two genera that presented major ambiguities in the ancestral state reconstructions of tendril type (*Bignonia* and *Tanaecium*). Our sampling scheme further included one species with multifid tendrils (*A. buccinatorium*), one species with hooked and uncinate tendril tips (*D. unguis-cati*), and two species with adhesive discs at the tendril tip (*A. buccinatorium* and *A. crucigerum*), such that a complete picture of tendril development in Bignonieae could be obtained. Vouchers for all sampled taxa are presented in Table 2.

Ontogenetic studies

Shoot apices were collected from mature plants, producing fully adult leaves. These apices were fixed under vacuum for 48 hours in glutaraldehyde and formaldehyde (Karnovsky, 1965) or 4% paraformaldehyde (Garcês & Sinha, 2009). Apices were dehydrated in a graded, ascending series of ethanol and critical-point dried with CO_2. Samples were then mounted on SEM stubs with epoxy, gold sputter-coated, and observed using SEM. For the histological investigations, shoot apices were dehydrated in a graded, ascending series of tertiary butanol and embedded in paraffin (Johansen, 1940). Embedded specimens were sectioned using a rotary microtome, then mounted on slides and stained with toluidine blue (O'Brien et al., 1964). Sections were permanently sealed with Permount (Fisher Scientific, Pittsburgh, Pennsylvania, U.S.A.).

RESULTS

ANCESTRAL CHARACTER STATE RECONSTRUCTIONS OF TENDRIL TYPE

Maximum parsimony reconstructions

Parsimony ancestral character state reconstructions of tendril type using the all-most-parsimonious states trace option support that the ancestral condition for the tribe is ambiguous, with trifid tendrils representing the ancestral condition of the Core Bignonieae clade (all Bignonieae, excluding *Perianthomega* Bureau ex Baill.). Simple tendrils have evolved at least three times from ancestors with trifid tendrils: once in the ancestor of *Adenocalymma* Mart. ex Meisn., once in the ancestor of *Bignonia*, and once in the ancestor of *Fridericia* and allies (Fig. 2). Further, at least three independent origins of multifid tendrils were reconstructed within *Bignonia*, *Manaosella* J. C. Gomes and *Neojobertia* Baill. A single evolution of bifid tendrils was hypothesized within *Tanaecium pyramidatum*, which bears both bifid and trifid tendrils. Furthermore, tendrils have been lost in 11 taxa: once in *Anemopaegma* Mart. ex Meisn. and once in *Mansoa*, both from trifid-tendrilled ancestors; twice in *Adenocalymma*, five times in *Fridericia*, once in *Xylophragma* Sprague,

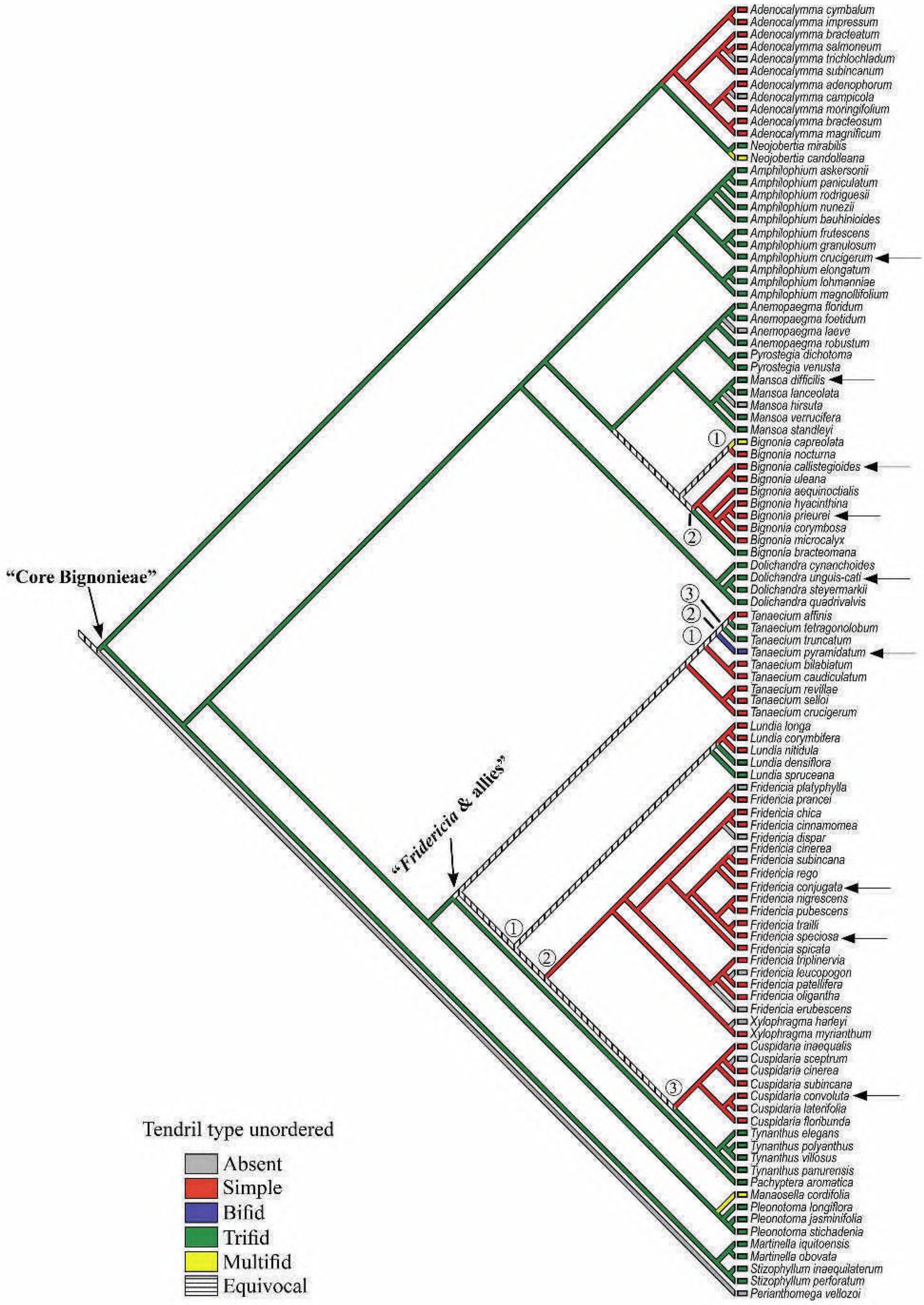


Figure 2. Single optimum maximum likelihood tree derived from the analysis of combined *ndhF* and *PepC* sequences of 104 species of Bignonieae (from Lohmann, 2006) plus *Perianthomega vellozoi*, with parsimony ancestral state reconstruction of the character "tendril type" showing all ambiguous reconstructions. Arrows indicate the phylogenetic placement of species selected for the ontogenetic study, except for *Amphilophium buccinatorium* and *Fridericia samydoides*, which were not included in this phylogeny. Clade names are modified from Lohmann (2006). Circled number = internal node number "n." Color-coded figure legend summarizes the five character states of tendril type in Bignonieae.

Table 2. Taxa sampled for ontogenetic study, with voucher detail for collectors, localities, and herbaria of deposit.

Taxon	Collection number (herbarium)	Locality
Bignonia prieurei DC.	*Zuntini 13* (CVRD, SPF)	BRAZIL. **Espírito Santo:** Linhares, Nat. Res. Companhia Vale do Rio Doce.
B. callistegioides Cham.	*Sousa-Baena 3* (DAV)	U.S.A. **California:** Davis, UC-Davis Arboretum, Terrace Garden.
Cuspidaria convoluta (Vell.) A. H. Gentry	*Pace 48* (SPF)	BRAZIL. **São Paulo:** Nova Odessa, Plantarum Bot. Gard.
Fridericia conjugata (Vell.) L. G. Lohmann	*Pace 44* (SPF)	BRAZIL. **São Paulo:** Nova Odessa, Plantarum Bot. Gard.
F. samydoides (Cham.) L. G. Lohmann	*Pace 49* (SPF)	BRAZIL. **São Paulo:** Nova Odessa, Plantarum Bot. Gard.
F. speciosa Mart.	*Pace 40* (SPF)	BRAZIL. **São Paulo:** Nova Odessa, Plantarum Bot. Gard.
Tanaecium pyramidatum (Rich.) L. G. Lohmann	*Pace 14* (SPF) *Pace 35* (SPF)	BRAZIL. **São Paulo:** São Paulo, Nat. Res. Univ. São Paulo.
Dolichandra unguis-cati (L.) L. G. Lohmann	*Groppo 322* (SPF)	BRAZIL. **São Paulo:** São Paulo, Nat. Res. Univ. São Paulo.
Mansoa difficilis (Cham.) Bureau & K. Schum.	*Pace 35* (SPF)	BRAZIL. **São Paulo:** São Paulo, Nat. Res. Univ. São Paulo.
	Zuntini 4 (CVRD, SPF)	BRAZIL. **Espírito Santo:** Linhares, Nat. Res. Companhia Vale do Rio Doce.
Amphilophium crucigerum (L.) L. G. Lohmann	*Pace 1* (SPF)	BRAZIL. **São Paulo:** São Paulo, Nat. Res. Univ. São Paulo.
A. buccinatorium (DC.) L. G. Lohmann	*Sousa-Baena 4* (DAV)	U.S.A. **California:** Davis, UC-Davis campus.

and once in *Cuspidaria*, all from simple-tendrilled ancestors.

Ambiguous reconstructions of tendril type are observed in the ancestral node of *Bignonia* and at the earliest diverging lineages of *Fridericia* and allies (which encompasses *Fridericia*, *Tanaecium*, *Lundia* DC., *Xylophragma*, *Cuspidaria*, and *Tynanthus* Miers; Fig. 2). Most of these ambiguities are resolved as simple tendrils under ACCTRAN optimization, except for the ancestor of *Lundia*, whose tendril type was reconstructed as trifid (Fig. 3A; Table 3). On the other hand, all ambiguities are resolved as trifid tendrils under DELTRAN optimizations (Fig. 3B; Table 3). The trifid tendril condition reconstructed at the ancestor of *Fridericia* and allies by DELTRAN implies six independent origins of simple tendrils within this clade (three independent origins in *Tanaecium*, one in *Lundia*, one in *Fridericia*, and one in *Cuspidaria*; Fig. 3B). On the other hand, the simple tendril condition reconstructed by ACCTRAN for the ancestor of *Fridericia* and allies implies three subsequent origins of trifid tendrils (one in *Lundia*, one in *Tanaecium*, and one in *Tynanthus*; Fig. 3A).

Overall, five evolutionary shifts to simple tendrils from ancestors with trifid tendrils are hypothesized under ACCTRAN, while nine shifts to simple tendrils from ancestors with trifid tendrils are hypothesized under DELTRAN (Fig. 3; Table 4). Furthermore, three independent evolutionary origins of multifid tendrils are hypothesized under ACCTRAN and DELTRAN, two of which are derived from ancestors with trifid tendrils and one of which is derived from an ancestor with simple tendrils under ACCTRAN optimization criteria, while under DELTRAN all multifid tendrils are derived from ancestors with trifid tendrils. In addition, at least four reversals to trifid tendrils from simple tendril ancestors are hypothesized under ACCTRAN, while a single evolution of trifid tendrils (no reversals) is hypothesized under DELTRAN, suggesting that trifid tendrils might be homologous in all lineages. A single evolutionary shift to bifid tendrils arising from an ancestor with trifid tendrils is hypothesized within *Tanaecium* under DELTRAN optimization criteria. However, ACCTRAN optimization fails to reconstruct the ancestor of an internal node of *Tanaecium* that gives rise to a heterogeneous clade that includes taxa with bifid, trifid, and simple tendrils, respectively, while DELTRAN optimization reconstructed a trifid-tendrilled ancestor for this clade.

Maximum likelihood reconstructions

ML optimizations of the character tendril type (Fig. 4) reconstructed an ancestral Bignonieae with absent

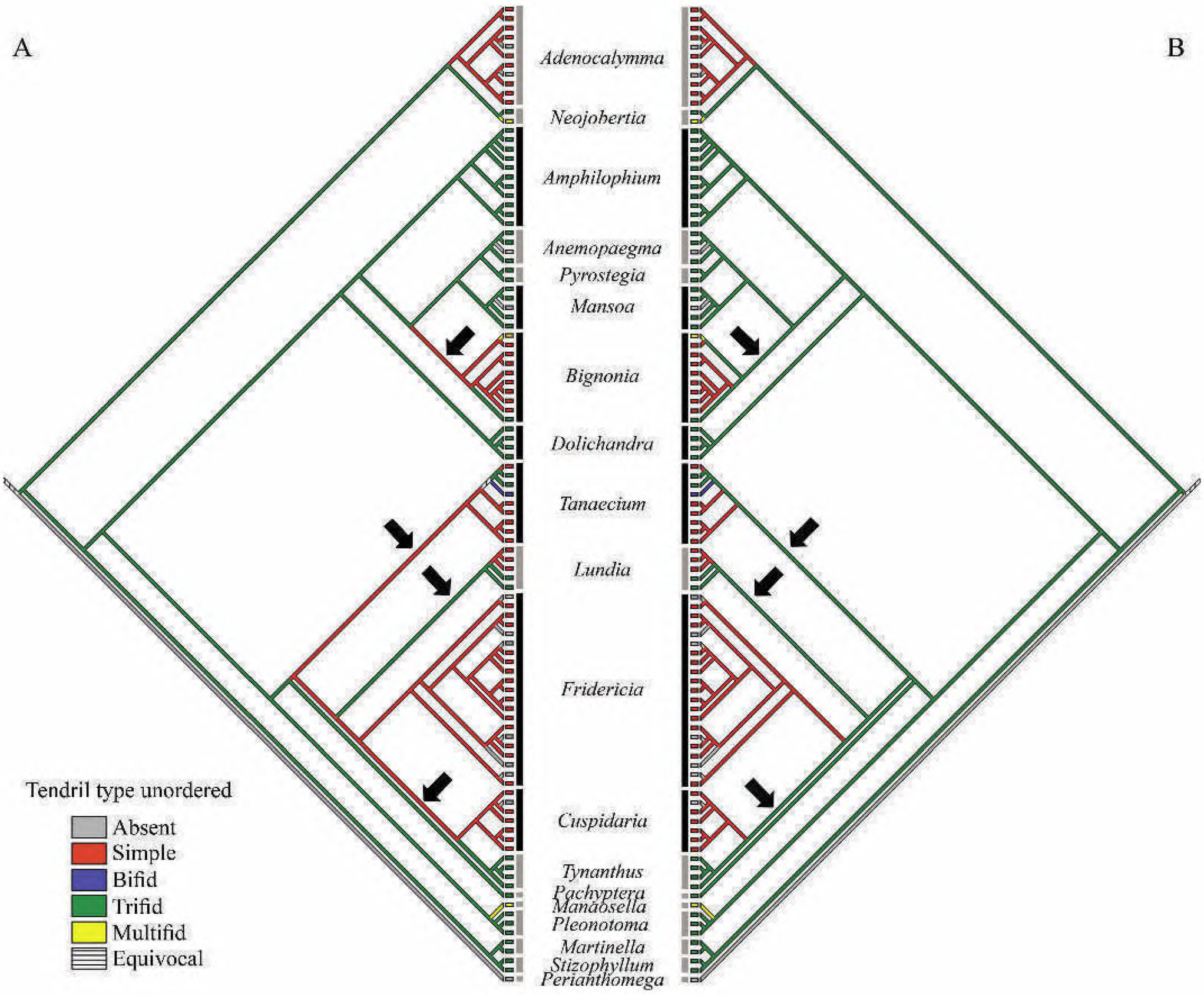


Figure 3. Single optimum maximum likelihood tree derived from the analysis of combined *ndhF* and *PepC* sequences of 104 species of Bignonieae (from Lohmann, 2006) plus *Perianthomega vellozoi*, with parsimony ancestral state reconstruction of the character "tendril type." —A. ACCTRAN optimization. —B. DELTRAN optimization. Black bars indicate the genera selected for the ontogenetic study, and black arrows indicate branches with equivocal reconstructions under the "all-most-parsimonious states" trace option. Color-coded figure legend summarizes the five character states of tendril type in Bignonieae.

tendrils (53%). The ancestral node of the Core Bignonieae was reconstructed as being trifid (78%), from which there have been seven evolutionary shifts to simple tendrils (one in *Adenocalymma*, two in *Bignonia*, one in the ancestral node of *Cuspidaria* and *Fridericia*, two in *Tanaecium*, and one in *Lundia*) from ancestors that presented trifid tendrils. One reversal to trifid tendrils was found in *Tanaecium*. Furthermore, three independent origins of multifid tendrils (in *Bignonia*, *Neojobertia*, and *Tanaecium*), and one shift to bifid tendrils (within *Tanaecium*) are also hypothesized. In addition, there have been reversals to "absent tendrils" in several taxa: once in *Anemopaegma*, once in *Mansoa*, twice in *Adenocalymma*, five times in *Fridericia*, once in *Xylophragma*, and once in *Cuspidaria*.

ML reconstructed the tendril condition for the most recent ancestor of the clade that includes *Anemopaegma/Mansoa/Pyrostegia* C. Presl/*Bignonia* as trifid (98.77%). The tendril condition at deep nodes within this clade was also reconstructed as trifid, as was the tendril condition of the ancestor of *Bignonia* (72%; see pie chart in Fig. 4). Furthermore, two independent evolutionary shifts to simple tendrils were hypothesized within *Bignonia*. On the other hand, the ML reconstruction of tendril type suggested that the ancestor of *Fridericia* and allies likely presented trifid tendrils (58%), as did the direct ancestors of *Lundia* (79.6%) and *Tynanthus* (98.2%) within this lineage. Four shifts to simple tendrils from trifid tendrils occurred, one in the ancestor of *Fridericia/Xylophragma/Cuspidaria*, one in an internal node of *Lundia*, and two in *Tanaecium* (one in the genus ancestral node and one in an internal node). A simple-tendrilled ancestor in *Tanaecium* was strongly supported (85%), with its direct ancestor being poorly supported as simple (40% simple, 25% bifid, and 32% trifid; see pie chart in Fig. 4).

Table 3. Tendril types reconstructed at the ancestral node of clades with ambiguous reconstructions under simple parsimony reconstructions. Data for the Bayesian ancestral reconstructions were retrieved from Lohmann et al. (in prep.). For the exact placement of the individual internal nodes, refer to Figure 2. AN = ancestral node; IN = internal node; "—" = inexistent node.

		DELTRAN	ACCTRAN	ML	BAYESIAN
Fridericia and allies	AN	trifid	simple	trifid	simple
	IN 1	trifid	simple	trifid	simple
	IN 2	trifid	simple	simple	simple
	IN 3	trifid	simple	simple	simple
Tanaecium	AN	trifid	simple	simple	simple
	IN 1	trifid	simple	simple	simple
	IN 2	trifid	ambiguous	simple	—
	IN 3	trifid	trifid	trifid	simple
Lundia	AN	trifid	trifid	trifid	simple
Bignonia	AN	trifid	simple	trifid	simple
	IN 1	trifid	simple	simple	simple
	IN 2	trifid	simple	trifid	simple

TENDRIL DEVELOPMENT

All species studied herein have 2-foliolate leaves, with the terminal leaflet modified into a simple, trifid, or multifid tendril. In addition, one species with hooked tendril tips (*Dolichandra unguis-cati*) and two species with adhesive discs at the tendril tip (*Amphilophium buccinatorium* and *A. crucigerum*) were also sampled. In all species studied, the leaf primordia emerge from the flanks of the shoot apex as a rounded protuberance (Figs. 5E, G, 6G), and become more triangular and flattened as development progresses (Figs. 5A, 6A, E, 7A, 10A). At the second stage of development (P2), leaflets are already defined in the leaf primordium, and the tendril is evident as the distal terminal part of the leaf primordium. Because the plants are 2-foliolate, and the tendril represents a modified terminal leaflet (Fig. 1B–D), the tendril is already discernible as the leaflets differentiate from the

Table 4. Number of evolutionary shifts for each tendril type under different ancestral character state reconstructions. Data for the Bayesian ancestral state reconstructions were retrieved from Lohmann et al. (in prep.).

	Tendril type			
	Simple	Bifid	Trifid	Multifid
ACCTRAN	5 five evolutionary shifts from an ancestor with trifid tendrils	1 one evolutionary shift from an ancestor with ambiguous reconstruction	5 one evolutionary shift at the base of Bignonieae, with four reversals from ancestors with simple tendrils	3 two evolutionary shifts from ancestors with trifid tendrils and one shift from an ancestor with simple tendrils
DELTRAN	9 nine evolutionary shifts from ancestors with trifid tendrils	1 one evolutionary shift from an ancestor with trifid tendrils	1 one evolutionary shift at the base of Bignonieae, with no reversals	3 three evolutionary shifts from ancestors with trifid tendrils
ML	7 seven evolutionary shifts from ancestors with trifid tendrils	1 one evolutionary shift from an ancestor with simple tendrils	3 one evolutionary shift at the base of Bignonieae, with two reversals from ancestors with simple tendrils	3 two evolutionary shifts from ancestors with trifid tendrils and one from an ancestor with simple tendrils
BAYESIAN	6 five evolutionary shifts from ancestors with trifid tendrils and one shift from an ancestor with multifid tendrils	1 one evolutionary shift from an ancestor with trifid tendrils	4 one evolutionary shift at the base of Bignonieae, with three reversals from ancestors with simple tendrils	3 two evolutionary shifts from ancestors with trifid tendrils and one shift from an ancestor with simple tendrils

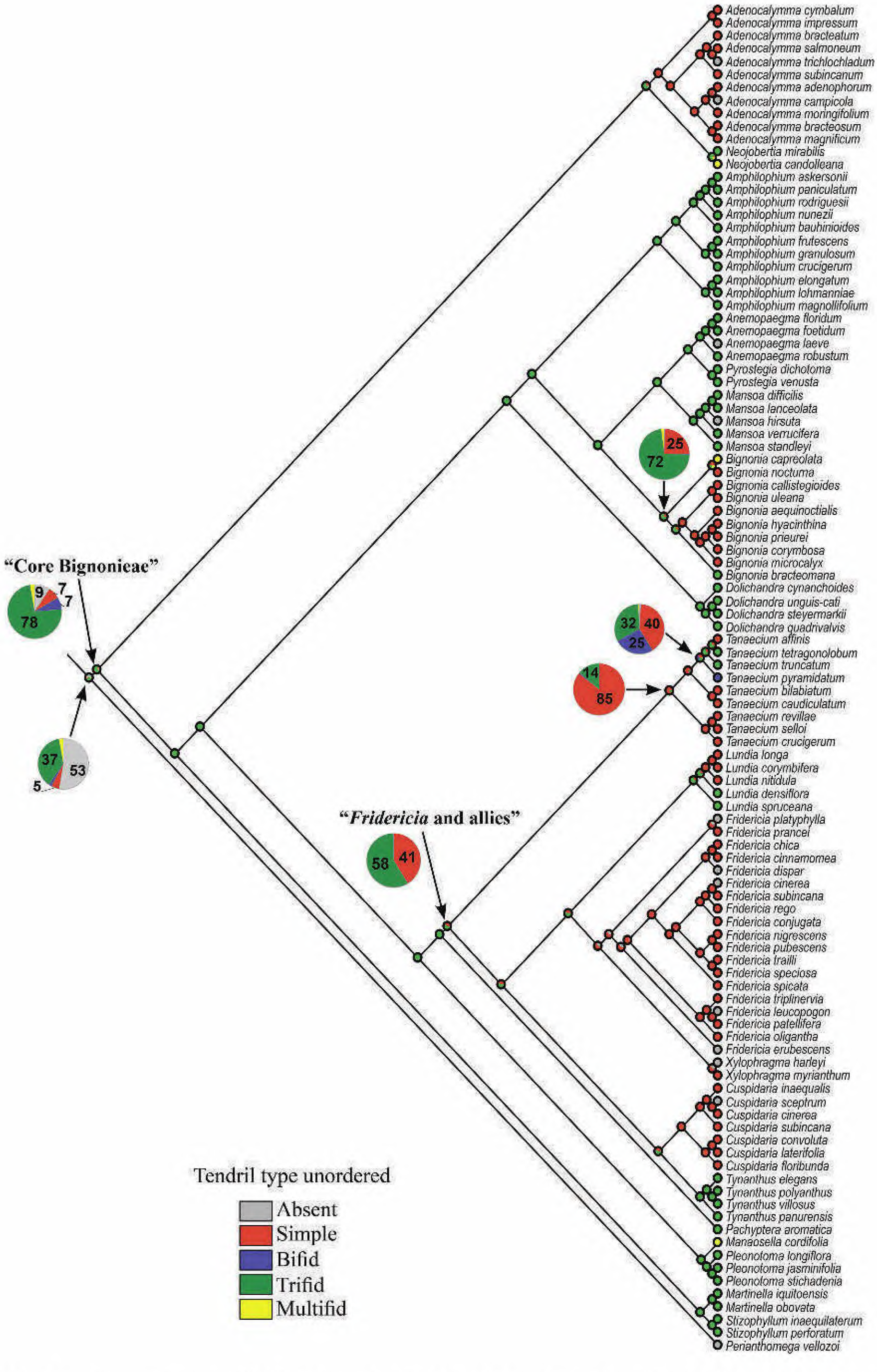


Figure 4. Single optimum maximum likelihood tree derived from the analysis of combined *ndhF* and *PepC* sequences of 104 species of Bignonieae (from Lohmann, 2006) plus *Perianthomega vellozoi*, with maximum likelihood ancestral state reconstruction of the character "tendril type." Pie charts are proportional to the likelihoods of the individual reconstructions. Numbers associated with pie charts are the likelihood values of the various tendril types. Color-coded figure legend summarizes the five character states of tendril type in Bignonieae.

base at the first stage of development (P1) (Figs. 5B, C, F, 6B, F, 7A, 8A, 10A). Independent of the tendril type, the leaf primordia always develop acropetally.

In all simple-tendrilled species studied (*Bignonia callistegioides*, *B. prieurei*, *Cuspidaria convoluta*, *Fridericia conjugata*, *F. samydoides*, and *F. speciosa*) the epidermis becomes precociously covered by

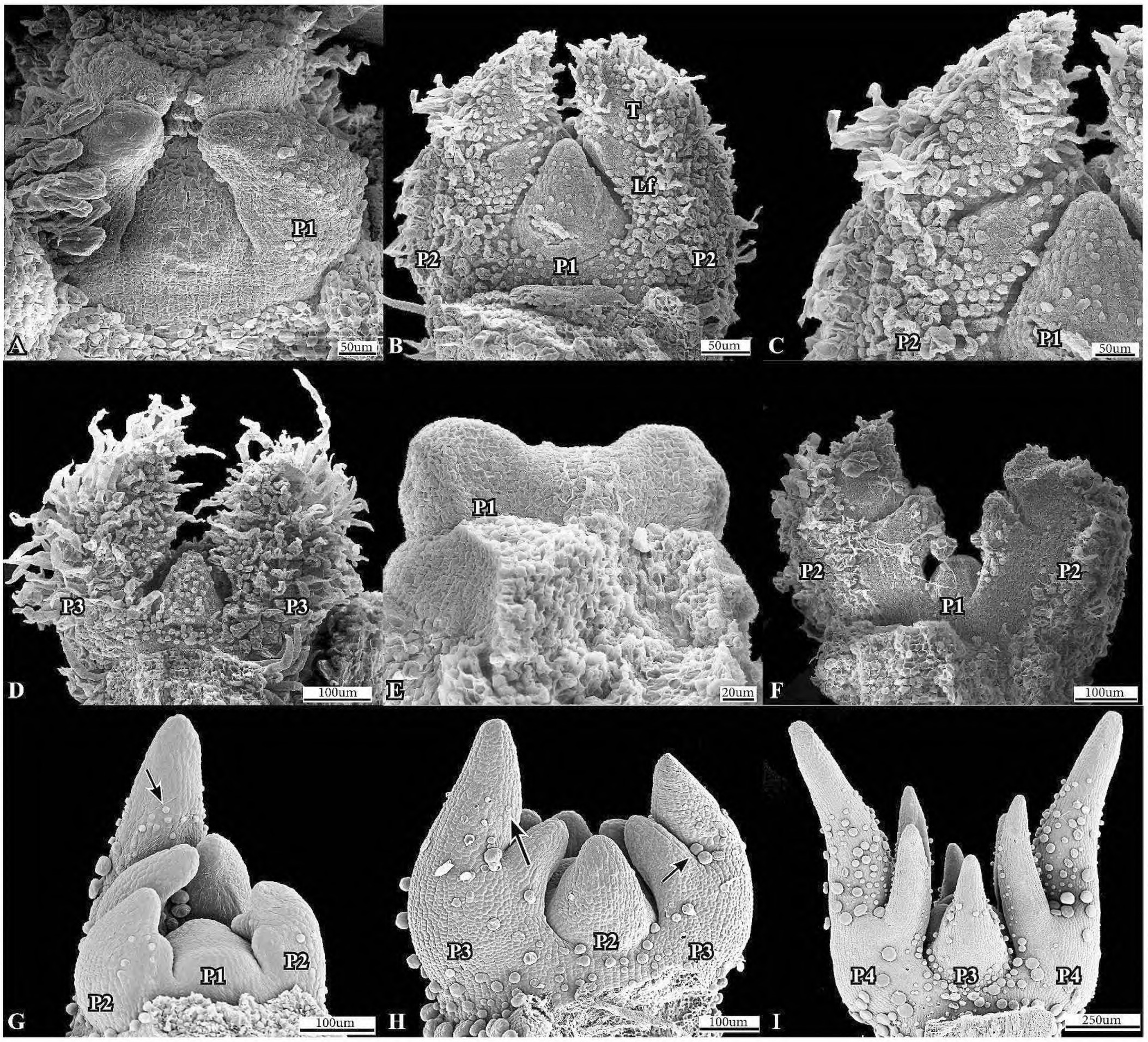


Figure 5. SEM micrographs of shoot apices illustrating the pattern of leaf development in representatives of Bignonieae with simple tendrils. A–D. *Fridericia speciosa* (*Pace 40*, SPF). —A. Shoot apex with P1. —B. Shoot apex with P2. —C. Detail of P2, showing epidermal differentiation in the adaxial surface of the tendril epidermis. —D. Shoot apex with P2 and P3, abaxial and adaxial surfaces of the P3 epidermis covered by trichomes. E, F. *Fridericia conjugata* (*Pace 44*, SPF). —E. Shoot apex with P1. —F. Shoot apex with P2. Abaxial surface of the epidermis of a P2 tendril showing a high degree of differentiation, and adaxial surface starting to develop trichomes. G–I. *Bignonia callistegioides* (*Sousa-Baena 3*, DAV). —G. Shoot apex with P1, P2, and P3. Arrow indicates trichome differentiation in the adaxial surface of P3 tendril epidermis —H. Shoot apex showing P3 in lateral view. Arrows indicate trichomes. —I. Shoot apex with P3 and P4, illustrating P4 with well-developed leaflets and tendrils and a higher degree of differentiation in the tendril epidermis. Lf = leaflet, T = tendril. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

trichomes during leaf development (Figs. 5B, F, 6B, G, H), indicating early loss of organogenetic capacity. This differentiation wave starts at the abaxial surface and continues toward the adaxial surface (Figs. 5A, G, 6A). At P2, leaf primordia show well-developed trichomes on the abaxial surface of the epidermis as well as developing trichomes on the adaxial surface (Figs. 5B, C, 6B, H). Leaf primordia become progressively covered by trichomes, and both the abaxial and adaxial surfaces of the epidermis show a higher degree of differentiation by the third stage of development (P3) (Figs. 5D, G, 6C, D, I). By P3, most species already have tendril tips covered by trichomes, except for *B. callistegioides* in which the tendril tip is always glabrous (Fig. 5I). In *B. prieurei*, the most pubescent species sampled, the abaxial surface of the epidermis already presents a high density of trichomes at P1, while both surfaces of the epidermis are already completely covered by developing peltate trichomes at P2; these trichomes mature in P3 (Fig. 6A–D).

In all studied species with branched tendrils (*Amphilophium buccinatorium*, *A. crucigerum*, *Dolichandra unguis-cati*, *Mansoa difficilis*, and *Tanae-*

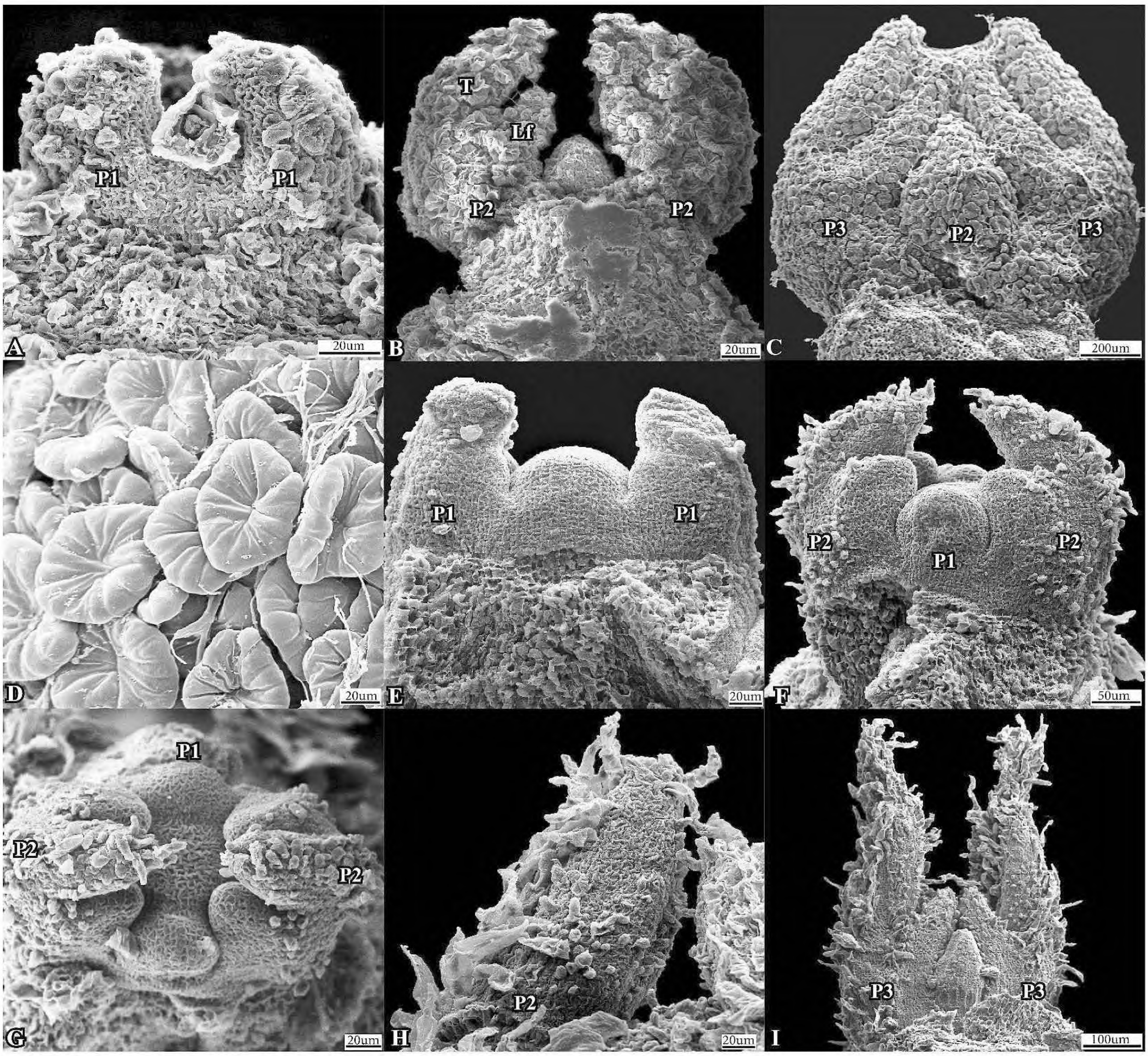


Figure 6. SEM micrographs of shoot apices illustrating the pattern of leaf development in representatives of Bignonieae with simple tendrils. A–D. *Bignonia prieurei* (*Zuntini 13*, SPF). —A. Shoot apex with P1. —B. Shoot apex with P2, showing leaf epidermis completely differentiated and covered by peltate trichomes. —C. Shoot apex with P2 and P3. —D. Shoot apex with P3, showing detail of a peltate trichome. E–I. *Cuspidaria convoluta* (*Pace 48*, SPF). —E. Shoot apex with P1. —F. Shoot apex with P2. —G. Frontal view of shoot apex, showing epidermal differentiation in P2, mainly in the abaxial surface of the tendril epidermis. —H. Shoot apex with P2 showing tendril detail and trichomes starting to develop in the adaxial surface of the epidermis. —I. Shoot apex with P2 and P3, showing both surfaces of P3 epidermis covered by trichomes. Lf = leaflet, T = tendril. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

cium pyramidatum) leaflets are also clearly defined at P2, during which time all species start to develop trichomes on the surface of the leaf epidermis (Figs. 7A, B, 8A, 10A). As in the simple-tendrilled species, the differentiation of the epidermis is greater on the abaxial surface of the leaf primordium during the early stages of development. In *A. crucigerum*, *A. buccinatorium*, *D. unguis-cati*, and *M. difficilis*, the lateral branches of tendrils start to develop at late P2 (Fig. 7B), becoming well defined at P3 (Figs. 7A, C, 8B, 10B, C). In these species, the formation of tendril lateral branches involves tissues from the lateral flanks of the base of the tendril's primary branch (Figs. 7A–C, 8B, 10C). In taxa with branched tendrils, the rate of epidermal differentiation is generally slower than that observed in the species with simple tendrils (Figs. 7D, E, 8C–E), maintaining their organogenetic capacity for a longer period of time. Furthermore, tendril tips of the taxa with branched tendrils never develop trichomes (Figs. 7F, 8F, 10F). In *D. unguis-cati*, tendril tips curve away from the shoot apex in the fifth stage of development (P5) (Fig. 7E), becoming uncinate later, at the ninth stage of development (P9).

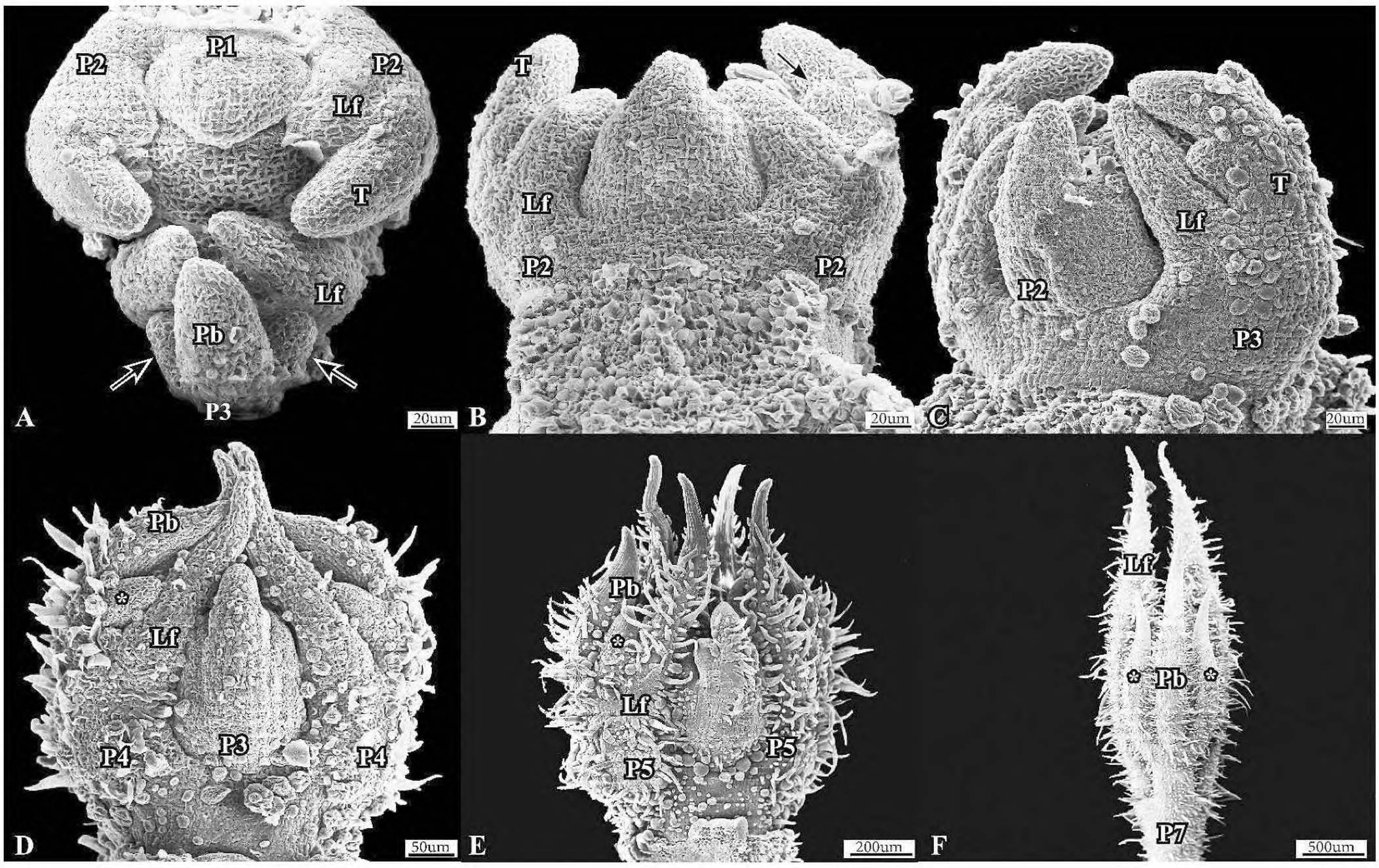


Figure 7. SEM micrographs of a shoot tip of *Dolichandra unguis-cati* (*Groppo 322*, SPF), showing the pattern of development in a trifid tendril. —A. Shoot apex with P1, P2, and P3. Arrows indicate the lateral branches of tendrils in P3. —B. Detail of early P2. Arrow indicates the tissue proliferation that will form the tendril lateral branches. —C. Shoot apex with P3, showing the epidermal differentiation in the tendrils. —D. Shoot apex with P4, showing well-developed tendril lateral branches and a higher degree of epidermal differentiation. —E. Shoot apex with P5, showing higher degree of differentiation, with primordia covered by tector and peltate trichomes. —F. Shoot apex with P7, showing tendril tips starting to become uncinate. Asterisks indicate tendril lateral branches. Lf = leaflet, T = tendril, Pb = tendril primary branch. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

In *Tanaecium pyramidatum*, on the other hand, the tendril lateral branches emerge from the adaxial surface of the tendril primary branch. In this species, the blastozone (i.e., the organogenetic competent region located in the lateral margins of the leaf primordia; Hagemann & Gleissberg, 1996) seems contracted, occupying only the adaxial portion of the tendril primordium. Contrary to the other species that bear branched tendrils, the lateral branches of *T. pyramidatum* are not clearly defined at P3 (Fig. 8H). At this stage, the tissue protuberance that gives rise to the tendril lateral branches arises at the base of the tendril primary branch (Fig. 8H, I). An elongation of the region below the branch insertion occurs during the transition from P3 to the fourth stage of development (P4), and the lateral branches are positioned at the tip of the tendril at P4 (Fig. 8J); however, tendrils are not yet clearly defined at this stage (Fig. 8K). It is only at the sixth stage of development (P6) that the lateral branches of these tendrils become clearly visible, although lateral tendril branches remain disproportionate in size relative to the primary tendril branch at this stage (Fig. 8L).

The leaf primordia of *Tanaecium pyramidatum* show an accelerated rate of epidermal differentiation (Fig. 8G) when compared to other species with branched tendrils (e.g., *Amphilophium buccinatorium*, *A. crucigerum*, *Dolichandra unguis-cati*, and *Mansoa difficilis*). At P3, trichome density is high, reaching the tendril tip, with the region where the lateral branches arise remaining as the only glabrous portion. The degree of epidermal differentiation continues to increase during development, with the entire leaf surface (including the tip of the lateral branches of the tendril) being covered by trichomes by P6 (Fig. 8L). The other branched, tendrilled species (i.e., *A. buccinatorium*, *A. crucigerum*, *D. unguis-cati*, and *M. difficilis*) present tendril tips that remain glabrous until more advanced stages of development (Figs. 7F, 8F, 10F). The timing of differentiation of the epidermis of the tendrils of *T. pyramidatum* resembles the pattern seen in species with simple tendrils (i.e., *Bignonia callistegioides*, *B. prieurei*, *Cuspidaria convoluta*, *Fridericia conjugata*,

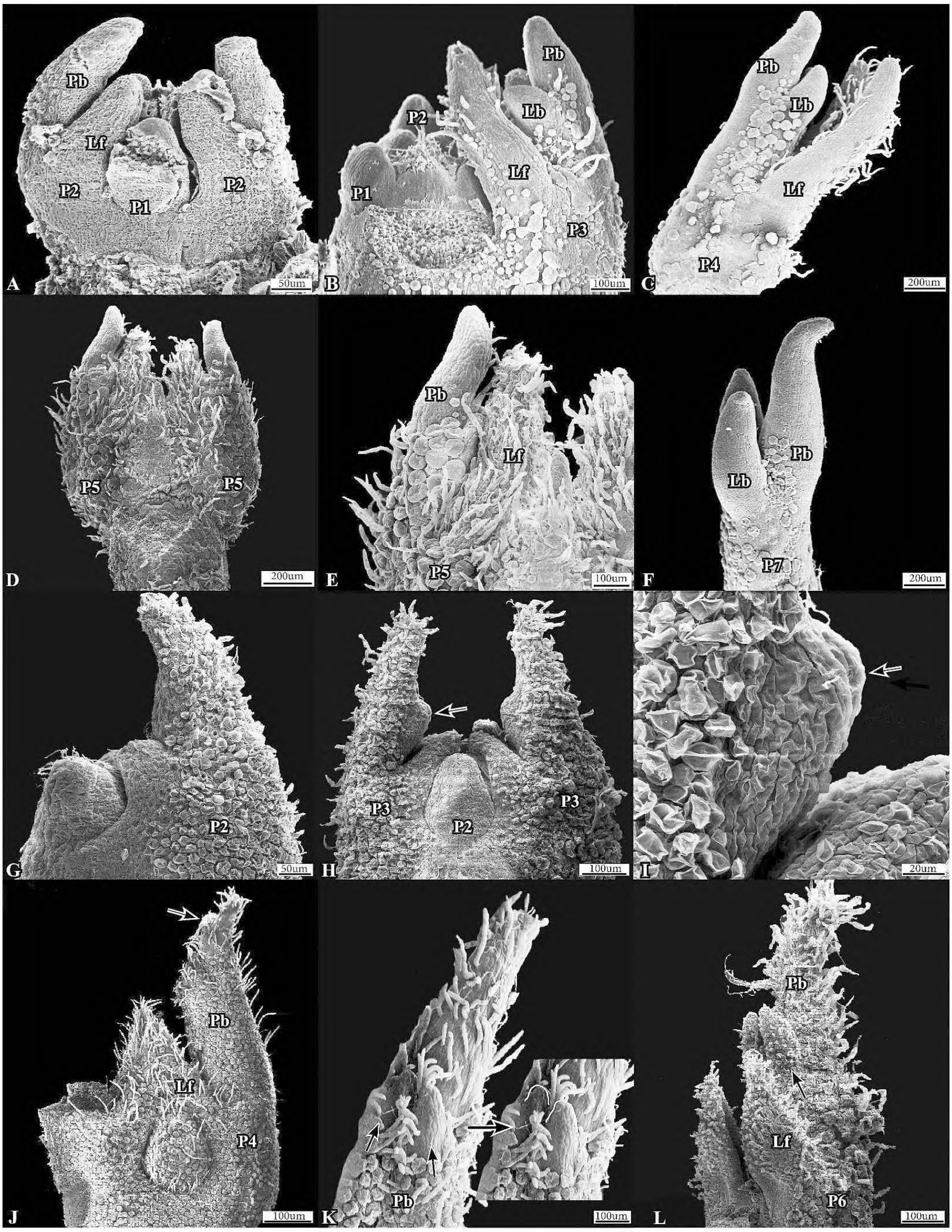


Figure 8. SEM micrographs of shoot apices illustrating the pattern of leaf development in representatives of Bignonieae with trifid tendrils. A–F. *Mansoa difficilis* (*Zuntini 4*, SPF). —A. Shoot apex with P1 and P2, showing the tendril still unbranched at P2. —B. Shoot apex with P1, P2, and P3, showing the tendril with clearly defined branches at P3. —C. Shoot apex with P4, illustrating the well-developed tendril lateral branches. —D. Shoot apex with P5, with the degree of differentiation increasing drastically from P4 (previous figure) to P5. —E. Shoot apex with P5. Detail illustrates tector and peltate trichomes on the tendril epidermis. —F. Shoot apex with P7, with tendril detail showing glabrous branched tip. G–L. *Tanaecium pyramidatum* (*Pace 35*, SPF). —G. Shoot apex with late P2. Epidermis of tendril abaxial surface showing a high degree of differentiation. —H. Shoot apex with P2 and P3. Arrow indicates the tissue proliferation in the tendril primary branch that will lead to the formation of lateral branches at P3. —I. Detail of P3, showing the beginning of lateral branch formation. Arrow indicates the tissue proliferation in the adaxial surface of the tendril. The epidermis around the tissue protuberance is covered by trichomes. —J.

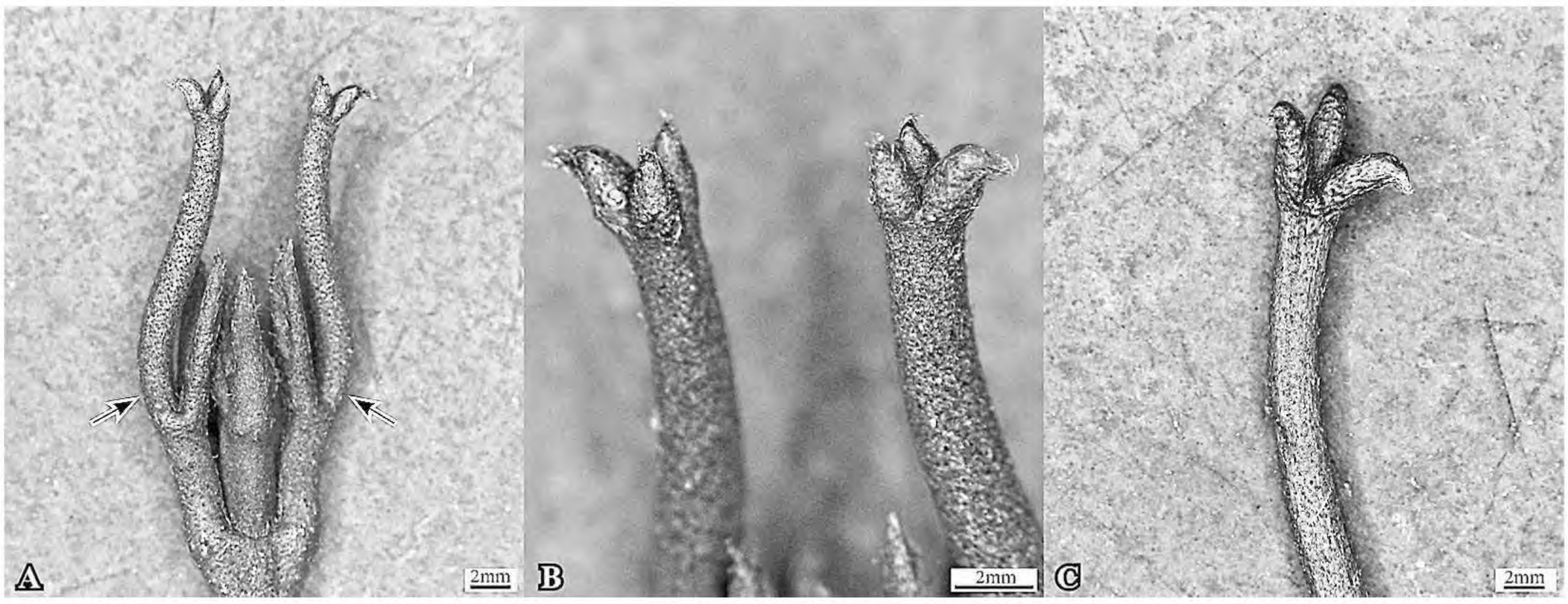


Figure 9. *Tanaecium pyramidatum* (*Pace 35*, SPF). —A. Shoot apex with P9 (arrows indicate P9). —B. Higher magnification of the tendril tip at P9. —C. P10, showing a detail of the tendril tip, and the three branches of the tendril with similar sizes.

F. samydoides, and *F. speciosa*). Although the lateral branches show a delayed onset, the three tendril branches present similar sizes by P9 (Fig. 9A, B). By the tenth stage of development (P10), the lateral branches are well developed and homogeneous in size (Fig. 9C).

Histological analyses indicate that the tissues that proliferate from tendril lateral branches have a different origin in *Tanaecium pyramidatum* when compared to the other branched, tendrilled species investigated. In *Amphilophium buccinatorium*, *A. crucigerum*, *Dolichandra unguis-cati*, and *Mansoa difficilis*, the tissue protuberance seems to originate from the epidermis and ground tissue (Fig. 11A, B). On the other hand, this tissue seems to be derived mainly from superficial layers in *Tanaecium* (Fig. 11C, D).

In *Amphilophium buccinatorium*, the only species with multifid tendrils investigated, the tertiary branches start to emerge from the primary tendril branch during P4, after the tendril lateral branches have already appeared (Fig. 10D, E). In this species, the lateral and tertiary tendril branches may develop in an asymmetrical manner, with tendril branches developing at different rates, resulting in a difference in size between the two lateral and/or tertiary branches (Fig. 10C, E). The ramifications of the secondary branches develop later, whenever present. The adhesive discs present in both species investigated for *Amphilophium* arise late in development, when leaves are already mature.

Discussion

We studied the evolution of tendrils with an integrated approach that combined ancestral character state reconstructions and detailed developmental data. The character tendril type was mapped onto a robust phylogeny of Bignonieae (Lohmann, 2006), using MP and ML assumptions. We further described tendril development in 11 species that were selected according to their phylogenetic placement and tendril morphologies (i.e., simple, trifid, and multifid tendrils). The interpretation of the ontogenetic data in light of the ancestral character state reconstructions provided key insights for the resolution of ancestral tendril types at nodes in which reconstructions were ambiguous and problematic, especially in *Bignonia* and *Tanaecium*. Below we discuss our results and raise hypotheses about evolutionary processes and molecular mechanisms that may have led to the great diversity of tendril types currently seen in Bignonieae.

Ancestral Character State Reconstructions

ML reconstructed an absent tendril condition for the ancestor of the entire tribe (53%), while MP reconstructions led to an ambiguous condition for the

←
Shoot tip with P4, showing epidermis covered by trichomes and presenting a high degree of differentiation. Tendril lateral branches not clearly defined (arrow). —K. P4, illustrating the tendril tip in detail. Arrows indicate the poorly defined lateral tendril branches. White lines delineate the limits of the lateral branches. —L. P6, showing primary branches and lateral branches (arrow) disproportionate in size and completely covered by trichomes. Lb = tendril lateral branch, Lf = leaflet, Pb = tendril primary branch. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

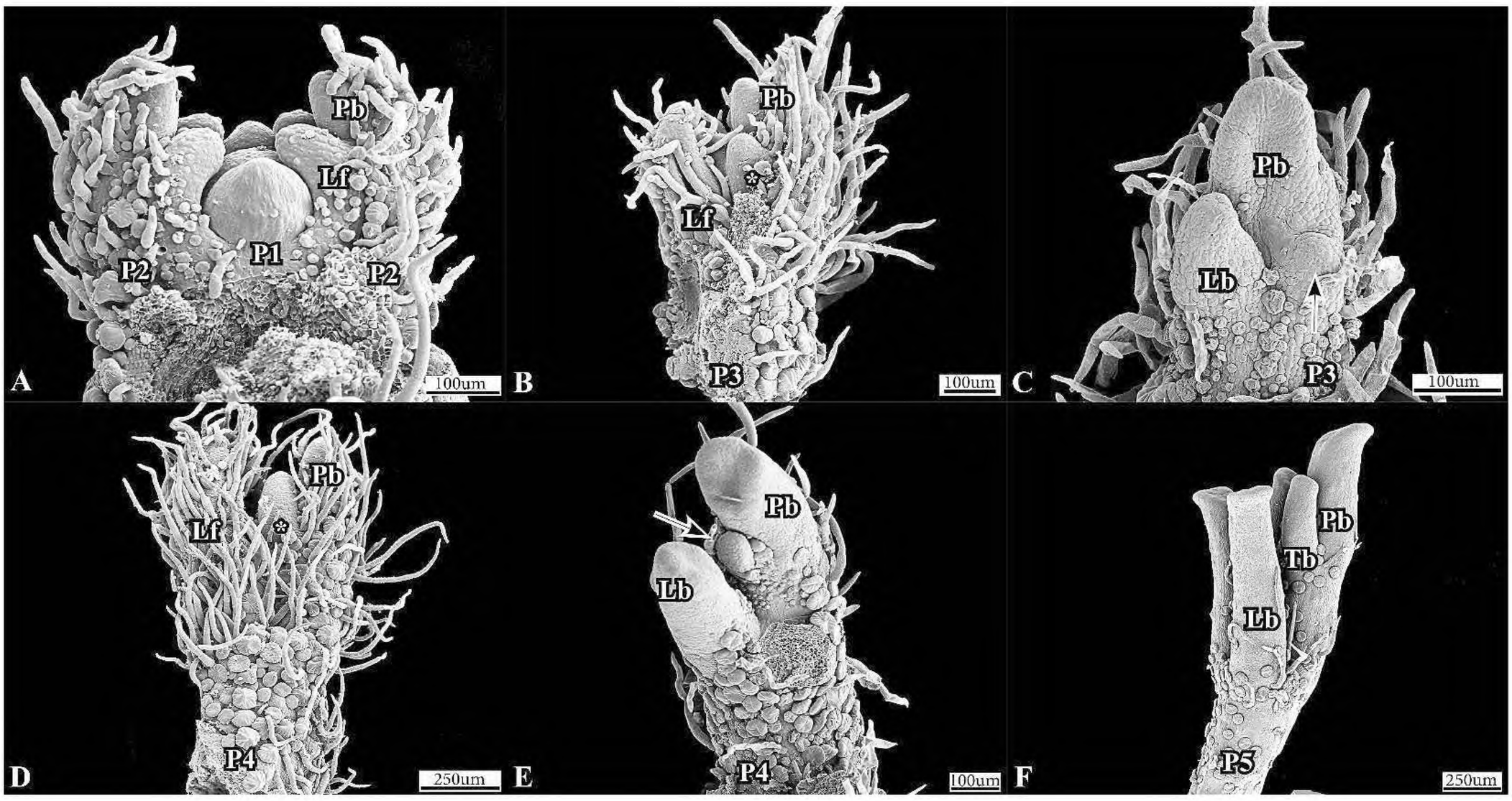


Figure 10. SEM micrographs of *Amphilophium buccinatorium* (*Sousa-Baena 4*, DAV), illustrating the development of a multifid tendril. —A. Shoot apex with P1 and P2. —B. P3 detached from shoot tip, showing the development of the lateral branches of the tendril (asterisk). —C. P3, showing the development of the asymmetrical lateral branches of the tendril (arrow). —D. P4, tendril lateral branches (asterisk) at a more advanced stage of development. Primordium covered by peltate and long tector trichomes. —E. P4, showing the asymmetrical development of the tertiary branches of the tendril (arrow). —F. P5, showing completely developed multifid tendrils. Lf = leaflet, Pb = tendril primary branch, Lb = tendril lateral branch, Tb = tendril tertiary branch. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

ancestor of Bignonieae. Both ML and MP reconstructed a trifid condition for the ancestor of the Core Bignonieae clade (78%). The trifid condition reconstructed for the ancestor of the Core Bignonieae clade corroborates ancestral character state reconstructions using Bayesian assumptions as conducted by Lohmann et al. (in prep.). However, Lohmann et al. did not include *Perianthomega* and thus did not reconstruct the ancestral condition for the whole tribe.

ML, ACCTRAN, and DELTRAN reconstructions hypothesized a single origin of bifid tendrils (most of which derived from an ancestor that presented trifid tendrils), and three evolutionary origins of multifid tendrils. However, DELTRAN reconstructions suggest that all three origins of multifid tendrils derived from ancestors that presented trifid tendrils, while ACCTRAN, ML, and the Bayesian reconstructions from Lohmann et al. (in prep.) favor two evolutionary changes to multifid tendrils from ancestors that presented trifid tendrils, and one evolutionary shift from an ancestor that presented simple tendrils.

The number of evolutionary origins for trifid tendrils varied across methods, with a single origin being hypothesized under DELTRAN, three origins under ML, four evolutionary events under Bayesian (Lohmann et al., in prep.), and five evolutionary origins under ACCTRAN. The ancestral tendril type for the Core Bignonieae clade was reconstructed as trifid under all methods, while the ancestor of the entire tribe was ambiguous in the parsimony reconstructions, with all subsequent reversals deriving from ancestors with simple tendrils. ACCTRAN reconstruction hypothesized five evolutionary origins of simple tendrils from ancestors that presented trifid tendrils; Bayesian reconstructions hypothesized five evolutionary origins of simple tendrils from ancestors that presented trifid tendrils (Lohmann et al., in prep.), while ML reconstructions hypothesized seven origins. Conversely, DELTRAN favored a much higher number of evolutionary origins for simple tendrils (nine), all of which were derived from ancestors that presented simple tendrils.

Overall, ACCTRAN and ML ancestral state reconstructions show similar patterns of tendril evolution. In contrast, DELTRAN optimizations consistently led to divergent scenarios. Most of the ambiguity associated with the ACCTRAN and DELTRAN reconstructions is associated with the ancestral tendril condition reconstructed for *Bignonia*, and with the tendril types reconstructed for the earliest diverging lineages of *Fridericia* and allies. In all instances, the same ancestral tendril types were reconstructed by ACCTRAN and Bayesian approach-

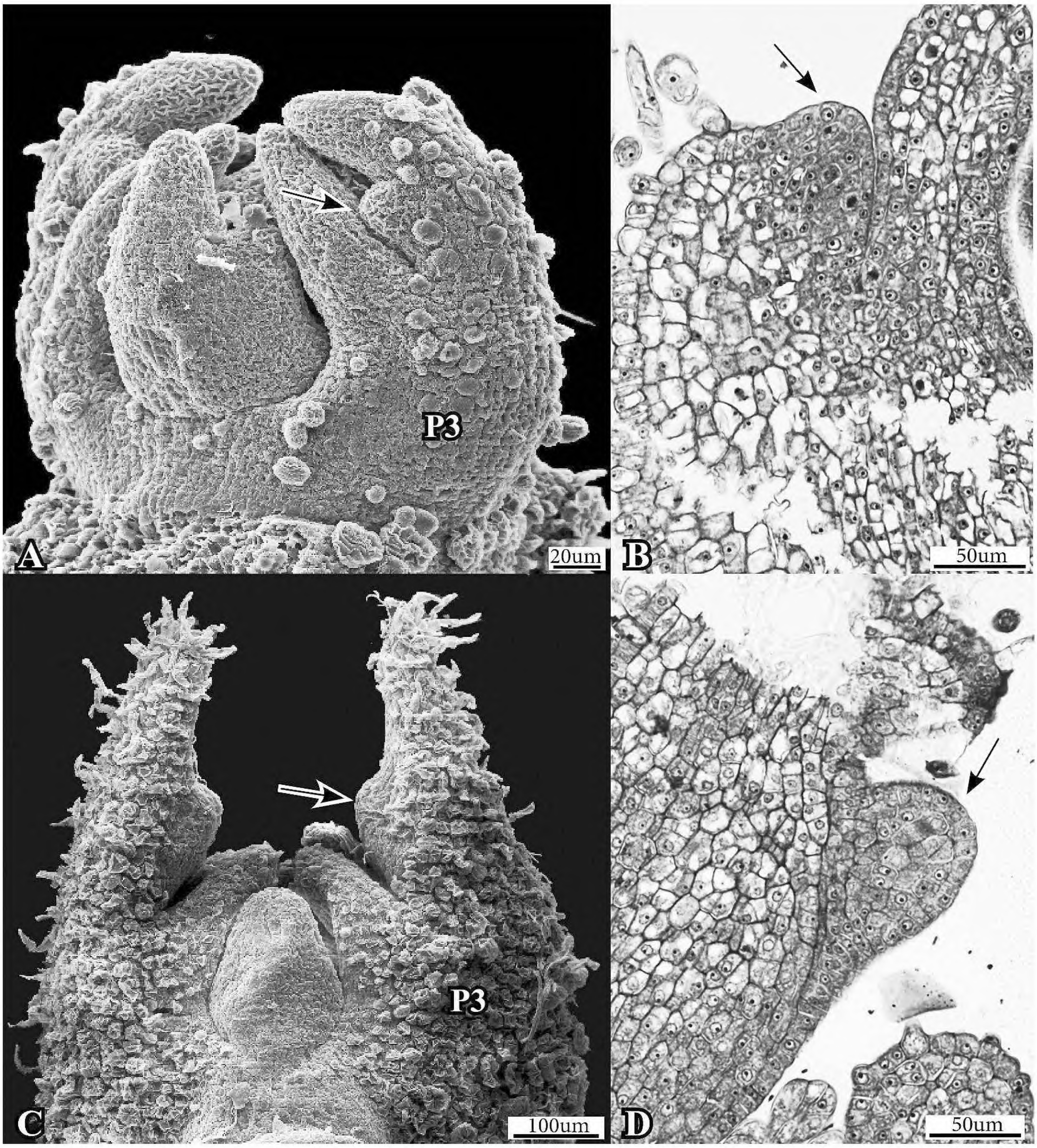


Figure 11. SEM micrographs and histological sections of leaf primordium of *Dolichandra unguis-cati* and *Tanaecium pyramidatum*. A, B. *Dolichandra unguis-cati* (*Groppo 322*, SPF). C, D. *Tanaecium pyramidatum* (*Pace 35*, SPF). —A, C. Shoot apices with P3, showing trifid tendril with tissue proliferation that will lead to the formation of the tendril lateral branches (arrows). —B, D. Longitudinal sections of the tissue bulge that will form the lateral tendril branches. —B. Formation of the tendril lateral branches (arrow) involving the division of cells in the epidermal and ground tissue. —D. Tissue that will give rise to tendril lateral branches (arrow) seems to have originated mainly from superficial layers. Developmental stage of the leaf primordia is indicated by Pn, where "n" gives the stage of development of the primordium in question.

es. On the other hand, ML hypothesized a trifid ancestor for *Bignonia* and *Fridericia* and allies, which is in agreement with the DELTRAN reconstructions (Table 3). While ACCTRAN optimizations accelerate changes toward the root of the tree, increasing the number of reversals, DELTRAN optimizations delay changes away from the root, increasing independent gains (Swofford & Maddison, 1987). Although DELTRAN and ACCTRAN optimizations were created as tools of equal value to infer evolutionary patterns, there has been a preference for resolving ambiguous reconstructions using ACCTRAN (Agnarsson & Miller, 2008). This preference is associated with the notion that reversals are more likely than

parallelisms and that the loss of complex traits is more likely than parallel gains (Pinna, 1991; Agnarsson & Miller, 2008). In this study in particular, ACCTRAN and ML reconstructions favored multiple evolutionary origins of trifid and simple tendrils, while DELTRAN favored a single evolutionary event for trifid tendrils and a much higher number of evolutionary steps for simple tendrils (at least nine). Even though the latter scenario is in agreement with the concept that loss of complex traits is more likely than repeated gains, in general all other reconstructions (ACCTRAN, ML, and Bayesian) and ontogenetic data do not favor this hypothesis.

The differences encountered between the various methods of ancestral character state reconstruction were not surprising, given that each of these methods is based on a different set of criteria and assumptions. For example, MP prioritizes the smallest number of evolutionary changes and favors the least complex explanations for an observation. On the other hand, model-based approaches, such as ML, favor the most probable explanations for a given dataset, which may or may not represent the most parsimonious explanations (Cunningham et al., 1998; Omland, 1999; Pagel, 1999). In general, different evolutionary scenarios are reconstructed with the employment of distinct reconstruction methods and assumptions, changing the way we interpret how evolutionary events have occurred and what mechanisms are responsible for them (Losos, 1999). Integrated approaches that combine ancestral character state reconstructions with ontogenetic data allow us to refine our evolutionary hypotheses as well as to pose subsequent hypotheses about the evolutionary processes and genetic mechanisms that can lead to the patterns of morphological diversity seen in extant species.

TENDRIL DEVELOPMENT

Blastozone activity

All species with simple tendrils studied here showed very similar patterns of development, including an early loss of organogenetic capacity and precocious epidermal differentiation during leaf development. On the other hand, leaf primordia of all species with branched tendrils studied (*Amphilophium buccinatorium*, *A. crucigerum*, *Dolichandra unguis-cati*, and *Mansoa difficilis*) present slower rates of epidermal differentiation and longer organogenetic capacity than species with simple tendrils. Furthermore, these species bear tendril branches that start to appear at late P2 (Fig. 7B), becoming clearly defined at P3 (Figs. 7A, C, 8B, 10B, C). Species with branched tendrils also show glabrous tendril tips at late stages of development.

In *Tanaecium pyramidatum*, on the other hand, the three tendril branches become clearly visible only at P6, and a delay in the development of the tendril lateral branches is observed when compared to the other species with branched tendrils. In addition, *T. pyramidatum* shows an accelerated rate of epidermal differentiation when compared with the other species with branched tendrils.

In most species with trifid tendrils (*Amphilophium crucigerum*, *Dolichandra unguis-cati*, and *Mansoa difficilis*) the pattern of activity of the blastozone during the formation of lateral branches of tendrils seems to be a reiteration of the activity pattern used to form leaflets. The blastozone is located in the same relative position (marginal) in the tendril primary branch as compared to the leaf primordium and shows a similar pattern of fractionation. Thus, maintenance of the organogenetic competent tissue (blastozone) with similar properties in the primary tendril branch may be responsible for the morphogenesis of the most common leaf type in Bignonieae. Likewise, the ramification pattern of the multifid tendrils of *A. buccinatorium* is not random. These tendrils are trifurcated several times, representing a reiteration of the initial pattern of activity found in the blastozone during leaflet formation.

Conversely, the blastozone is restricted to a portion of the adaxial surface of the tendril primary branch in *Tanaecium pyramidatum*. The epidermal differentiation program is activated earlier during the development of tendrils in *T. pyramidatum* than it is in the other trifid-tendrilled species of Bignonieae. On the other hand, the program to promote cell cycle activity in the blastozone is delayed in *T. pyramidatum* relative to other species with trifid tendrils. Thus, it is possible that the delay seen in the development of the lateral branches of *T. pyramidatum* may result from a disassociation between the differentiation/indeterminacy program and the genetic program that promotes cell cycle activity in the blastozone. Hence, when the cell-division cycle activity is triggered in the blastozone at P3, the intense epidermal differentiation that has already progressed restricts the blastozone to a small portion of the adaxial surface of the tendril. Consequently, tendril lateral branches in this species are derived from a smaller pool of meristematic cells, resulting in the formation of lateral and primary tendril branches that are disproportional in size (Fig. 8K, L).

Genes involved in the regulation of the blastozone activity

The degree of blade elaboration in compound leaves is determined by the complex and delicate

balancing of tissue differentiation and indeterminacy that is dynamically maintained during leaf development. Several genes regulate these processes, and the most general mechanism to maintain indeterminacy seems to involve the expression of *KNOX1* genes (Smith et al., 1992; Bharathan et al., 2002). More recently, *TCP* genes (another family of transcription factors) were found to also play an important role in the control of indeterminate identity during leaf development (Efroni et al., 2008). In particular, *TCP* genes were shown to play a major role in promoting tissue differentiation in the simple leaves of *Arabidopsis thaliana* (L.) Heynh. (Efroni et al., 2008). Furthermore, increases in *TCP* expression during the development of complex leaves of tomato result in a premature differentiation of leaf margins, leading to simplification of the leaf blade (Ori et al., 2007). One possible hypothesis to explain the interaction between *KNOX1* and *TCP* genes during leaf development is that the acquisition of *KNOX1* expression during compound leaf development, coupled with a fine adjustment of the expression of *TCP* genes, in a developmental stage-dependent manner, would regulate the degree of leaf differentiation as a whole and specify the regions in the blastozone that form lateral outgrowths (Floyd & Bowman, 2010; Koenig & Sinha, 2010).

Assuming that *KNOX1* and *TCP* genes perform essentially the same functions in Bignonieae, some changes in the expression of *TCP* genes must have occurred in *Tanaecium pyramidatum*. More specifically, the expression of *TCP* genes in earlier stages of development or an increased *TCP* expression may have caused early primordium differentiation and restriction of organogenetic competent tissue, resulting in a delay in the onset of the tendril lateral branches, as well as a delay in the rate of development.

In *Pisum sativum*, leaf development is controlled by *UNIFOLIOLATA/LEAFY* instead of *KNOX1* genes. In other species placed in the same clade (IRLC), leaf development is also controlled by *LEAFY*, with tendril development being directly associated with *TENDRILLESS* expression, a class I *HDZIP* gene (Hofer et al., 2001, 2009). Bignonieae tendrils are modified terminal leaflets that are similar to pea tendrils, suggesting that *LEAFY* could also represent a major regulator of leaf development in representatives of the tribe. However, *STM* (*KNOX1* gene) is expressed during leaf development in representatives of Bignonieae (Sousa-Baena et al., 2014), indicating that it is unlikely that *LEAFY* is the primary regulator of leaf development in representatives of Bignonieae.

ARP genes are responsible for the establishment of adaxial identity in developing leaves (Waites et al., 1998). In simple-leaved plants, *ARP* genes are expressed in the developing leaves, repressing the expression of *KNOX1* (Champagne & Sinha, 2004; McHale & Koning, 2004). However, in compound leaves of tomato, *KNOX1* and *ARP* have overlapping expression patterns, suggesting that both genes regulate meristematic functions during leaf development in this species (Kim et al., 2003). Silencing of *ARP* genes results in the formation of needle-like leaflets in several species of plants (Waites & Hudson, 1995; Schneeberger et al., 1998; Timmermans et al., 1999; Byrne et al., 2000; McHale & Koning, 2004). Even though needle-like leaflets are morphologically similar to tendrils, studies on the function of *ARP* genes in pea tendril development showed that this gene does not play an important role in the formation of tendrils in this species (Tattersall et al., 2005). Since pea leaf development is controlled by *LFY/FLO* rather than *KNOX1* genes, it is reasonable to assume that genes that interact directly with *KNOX1* also do not play key roles during leaf development in peas. However, *KNOX1* genes are expressed during leaf development of representatives of Bignonieae (Sousa-Baena et al., 2014), suggesting that interactions between *STM* and *ARP* genes may be involved in tendril determination in representatives of this clade. Moreover, other genes that regulate the establishment of abaxial/adaxial identity (e.g., *HD-zipIII* genes, *YABBY*, and *KANADI*) may play important roles in tendril development as well.

Alternatively, changes in the hormonal regulation during key leaf developmental stages might be responsible for the delayed development of tendril branches observed in *Tanaecium pyramidatum*. In particular, the production of auxin maxima induces the formation of leaflet primordia along the leaf margin (Barkoulas et al., 2008; Koenig et al., 2009; Floyd & Bowman, 2010; Koenig & Sinha, 2010). These auxin peaks are associated with the promotion of cell cycle activity and a shift in the plane of cell division, events that together lead to outgrowth of lateral organs (Koenig & Sinha, 2010). Hence, it is possible that a delayed auxin maximum might be associated with the delayed development of tendril lateral branches in *T. pyramidatum*.

INTEGRATING TENDRIL DEVELOPMENTAL DATA AND ANCESTRAL CHARACTER STATE RECONSTRUCTIONS

Four of the six simple-tendrilled species studied (*Cuspidaria convoluta*, *Fridericia conjugata*, *F. samydoides*, and *F. speciosa*) are placed within lineages with well-established simple tendrils. The

remaining two species (*Bignonia callistegioides* and *B. prieurei*) are within lineages whose ancestral tendril types are ambiguous. In addition, four species with branched tendrils are found in clades whose ancestors are unambiguously reconstructed as trifid (*Amphilophium buccinatorium*, *A. crucigerum*, *Dolichandra unguis-cati*, and *Mansoa difficilis*; Figs. 2–4). On the other hand, *Tanaecium pyramidatum*, another species with branched tendrils, is placed within a clade whose ancestor is ambiguously reconstructed as simple or trifid (Figs. 2–4; Table 1).

Most representatives of Bignonieae present 2-foliolate leaves, with the terminal leaflet modified into a tendril (Lohmann & Taylor, 2014). Ancestral state reconstructions of tendril type indicated that leaves without tendrils represent the ancestral condition in the tribe, which was followed by multiple evolutionary origins of different tendril types. However, ancestral state reconstructions of tendril type, based on different algorithms, led to ambiguous reconstructions in several nodes (Table 3). In particular, the ancestral tendril condition for *Bignonia* is ambiguous, as well as the ancestral tendril condition for the *Fridericia* clade (internal node in Fig. 2) and those of several lineages included herein. Because *Tanaecium* represents the earliest diverging lineage within the *Fridericia* clade, the resolution of the ancestral tendril condition for this genus is critical for a better understanding of the patterns of tendril evolution in all subsequent lineages.

As far as *Bignonia* is concerned, the tendril condition of the most recent ancestor of this clade was reconstructed as trifid under ML and DELTRAN optimizations, but as simple under ACCTRAN. Bayesian reconstructions corroborate the ACCTRAN reconstructions (Lohmann et al., in prep.). Ontogenetic studies of two species of *Bignonia* with simple tendrils (*B. callistegioides* and *B. prieurei*) indicated a developmental pattern for these species that is very similar to that of species of *Cuspidaria* and *Fridericia*, both of which belong to lineages with well-established, simple tendrils (i.e., homogeneous lineages in terms of tendril morphology, including simple-tendrilled species exclusively, and a clear simple-tendrilled direct ancestor). In particular, these species of *Bignonia* do not present any traces of lateral tendril branches that could be reminiscent of a trifid-tendrilled ancestor during development. Thus, the developmental data can be interpreted as support for early evolution of simple tendrils in the history of this genus, suggesting that the ancestral condition for *Bignonia* is simple tendril, corroborating the ACCTRAN and Bayesian ancestral character state reconstructions (Lohmann et al., in prep.).

As far as *Tanaecium* is concerned, DELTRAN optimizations reconstructed a trifid tendril condition for the ancestor of this clade, while ML and ACCTRAN reconstructed a simple tendril condition for the ancestor of this clade. Bayesian reconstructions (Lohmann et al., in prep.) corroborate the ML and ACCTRAN reconstructions. In the latter, the appearance of trifid tendrils in *Tanaecium* would represent subsequent reversal from simple tendrils. In this case, the simple-tendrilled ancestor would have suppressed the genetic program that leads to the formation of lateral branches (i.e., cell cycle activity in the blastozone). Ontogenetic studies of *T. pyramidatum* (a species with trifid tendrils) indicated that this genetic program was indeed reactivated in this species. However, this activation was delayed when compared to other trifid-tendrilled species. Furthermore, the pattern and rate of tendril differentiation in *T. pyramidatum* followed those found in lineages with well-established, simple tendrils (i.e., *Cuspidaria* and *Fridericia*), which includes early loss of organogenetic capacity. In other words, earlier stages of development in this species followed those of simple-tendrilled taxa, while later stages followed those of trifid-tendrilled species, leading to a mosaic of traits that are typical of simple-tendrilled taxa (i.e., rapid differentiation of the epidermis of the leaf primordia), and trifid-tendrilled taxa (i.e., the retention of organogenetic capacity in the primary branch of the tendril). While the reacquisition of trifid tendrils in this genus is homoplastic, it probably reflects some kind of underlying homology to form lateral branches that must have been retained from ancestral patterns of blastozone fractionation (Hall, 2003; Rutishauser & Moline, 2005). On the other hand, the retention of characteristics that are typical of simple tendrils in the earlier stages of development supports the hypothesis that its direct ancestor would have presented simple tendrils, thus favoring the ML, ACCTRAN, and Bayesian ancestral state reconstructions.

EVOLUTIONARY PROCESSES THAT MAY HAVE LED TO THE CURRENT DIVERSITY IN TENDRIL MORPHOLOGY

The emergence of a new area of scientific research, evolutionary developmental biology (Gilbert, 2003; Love & Raff, 2003), has prompted the reassessment of several classical concepts, such as homology, homoplasy, heterochrony, homeosis, heterotopy, and novelty (Muller & Wagner, 1991; Li & Johnston, 2000; Baum & Donoghue, 2002; Cronk, 2002; Hall,

2003; Rutishauser & Moline, 2005; Wagner et al., 2005). In particular, new findings about shared developmental pathways encountered among organisms that are not necessarily closely related led to new definitions of several of these classical concepts (Hall, 2003; Laubichler & Maienschein, 2003; Cracraft, 2005; Brigandt & Griffiths, 2007; Jaramillo & Kramer, 2007; Wagner, 2007). The excitement generated by the possibility of linking gene function to phenotype has brought new interpretation to classical concepts. This facilitates the analysis of developmental data in light of the newly available phylogenies and allows a better understanding of the evolution of development (Raff, 2000). Under this approach it is possible to infer how the dissociation between developmental modules could lead to evolutionary shifts, through processes like heterochrony, heterotopy, and homeosis (Li & Johnston, 2000; Baum & Donoghue, 2002; Cronk, 2002; Wagner et al., 2005).

As stated above (see discussion under *Blastozone activity*), the pattern of activity of the blastozone during the formation of tendril lateral branches in trifid-tendrilled species in Bignonieae seems to represent a reiteration of the pattern seen during the formation of leaflets. In the trifid-tendrilled species, the blastozone is situated in the same relative position (marginal) in the tendril primary branch when compared with the leaf primordium. On the other hand, the activity and position of the blastozone are different in *Tanaecium pyramidatum* when compared to those of other trifid-tendrilled species, with the lateral branches showing a delayed onset and growth rate.

In this context, it seems likely that the evolution of trifid tendrils in *Tanaecium* may have resulted from paedomorphosis by post-displacement (i.e., a delay in the onset of development of some organ or structure in the organism; Alberch et al., 1979). It is important to note that the term post-displacement was coined by zoologists (Alberch et al., 1979), whose study of organisms presents determinate growth and hence, if the heterochronic structure kept the same developmental rate seen in the ancestor, it would be smaller in the adult animal (Alberch et al., 1979; McNamara, 1986). However, plants have indeterminate growth, and sexual maturity cannot be used as an offset reference (Li & Johnston, 2000). Adult tendrils of *Tanaecium* have branches of equal size (Fig. 9C), which might result from a delayed developmental onset being consumed by the inherent capacity of plants for indeterminate growth.

Changes in the timing, rate, or spatial patterns of gene expression have been shown to represent one of the underlying causes of phenotypic variation (Raff, 1996; Tautz, 2002). Thus, the use of the term heterochrony was extended and is now also used to describe changes of the developmental timing at the molecular and genetic levels, apart from changes at the morphological level (Carroll, 2000). Heterochronic genes that specifically control developmental timing have been isolated in both plants and animals (Ambros & Horvitz, 1987; Slack & Ruvkun, 1998; Hunter et al., 2003; Chuck et al., 2007; Efroni et al., 2008; Sharbel et al., 2010).

In *Tanaecium*, heterochronic processes, such as a delay of the auxin maxima formation in the blastozone, coupled with an earlier onset of *TCP* expression, could be responsible for the evolution of trifid tendrils. Under this hypothesis, opposing types of heterochrony would be acting on tendrils, with post-displacement of auxin maxima formation and earlier onset of differentiation, resulting in a post-displaced development of tendril lateral branches. It is likely that much of the phenotypic variation that we see in extant species may have arisen through heterochronic processes (Gould, 1992). Indeed, the evolution of one single structure in a certain group of plants can be the result of several, and sometimes contrary, heterochronic processes acting in concert (Alberch et al., 1979; Li & Johnston, 2000).

Our results suggest that simple tendrils have evolved from trifid tendrils several times in Bignonieae. In these plants the epidermal differentiation is rapid, and the organogenetic competence appears to be lost early in development. Thus, changes in spatio-temporal patterns or levels of *TCP* expression could also be related to the precocious differentiation of the epidermis in simple-tendrilled species, and ultimately responsible for the arising of simple tendrils in Bignonieae. Indeed, it seems that a gradual loss of organogenetic competent tissue in leaf primordia over evolutionary time may have led to the current diversity of tendril morphology.

Conclusion

The interpretation of tendril ontogenetic data in light of a robust phylogenetic context revealed some interesting evolutionary trends. First, *Dolichandra* and *Mansoa* present trifid tendrils and arise within lineages whose immediate ancestors already had trifid tendrils. In these genera, the three tendril branches were already defined at P3. Second, *Tanaecium* belongs to a lineage whose immediate ancestors had simple tendrils. In this genus the three tendril branches are only clearly defined at P6 and a considerable delay in tendril development is observed when compared to species with trifid tendrils

whose immediate ancestors had trifid tendrils. In this species, tendril development is heterochronic, with the evolution of trifid tendrils involving the maintenance of simple tendril characteristics that were present in its ancestor, as well as the reacquisition of traits that are typical of trifid tendrils. Third, *Bignonia* presents the same developmental pattern as *Cuspidaria* and *Fridericia*, two genera that belong to lineages with well-established, simple tendrils, indicating that the evolution of simple tendrils happened early in the evolutionary history of these lineages.

Developmental studies contributed data that greatly improved the resolution of the ancestral character state reconstructions of tendril type in Bignonieae. These data corroborated ACCTRAN and Bayesian reconstruction in all instances and generally corroborated ML reconstructions, but did not support DELTRAN reconstructions in any instance. To date, detailed comparisons across methods of ancestral character state reconstructions are still limited, indicating the importance of using multiple methods when reconstructing ancestral character states. Furthermore, integrative approaches, i.e., combining data from multiple sources, are more likely to lead to more accurate ancestral character state reconstructions and more robust evolutionary hypotheses. Ideally, those hypotheses should be tested at a molecular level, involving spatio-temporal changes in gene expression that may have led to the patterns of phenotypic variation currently observed. Gene expression studies using in situ RNA hybridizations and comparing species with varied tendril morphologies are bringing new insights on the role of *STM*, *ARP*, and *LEAFY/FLORICAULA* genes in the regulation of tendril development in Bignonieae (Sousa-Baena et al., 2014). Further studies using gene silencing and gain-of-function approaches could also contribute important information for a better understanding of the function of those genes in Bignonieae.

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A NEW GENERIC CLASSIFICATION OF TRIBE BIGNONIEAE (BIGNONIACEAE)[1]

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ABSTRACT

The history of classification of the tribe Bignonieae and its genera are reviewed as context for a comprehensive new genus-level classification of the tribe Bignonieae (Bignoniaceae, Lamiales). This new classification is based on a well-supported phylogeny based on multiple molecular markers from both chloroplast and nuclear DNA, a morphological survey, and a broad sampling of taxa. Genera are circumscribed here as clades that are well supported as monophyletic by molecular data and also recognizable by one or more morphological synapomorphies. *Perianthomega* Bureau ex Baill. is here transferred from Bignoniaceae tribe Tecomeae into Bignonieae, and 21 genera and a total of 393 species are recognized in Bignonieae: *Adenocalymma* Mart. ex Meisn. (82 species), *Amphilophium* Kunth (47), *Anemopaegma* Mart. ex Meisn. (45), *Bignonia* L. (28), *Callichlamys* Miq. (1), *Cuspidaria* DC. (19), *Dolichandra* Cham. (8), *Fridericia* Mart. (67), *Lundia* DC. (13), *Manaosella* J. C. Gomes (1), *Mansoa* DC. (12), *Martinella* Baill. (2), *Neojobertia* Baill. (2), *Pachyptera* DC. ex Meisn. (4), *Perianthomega* (1), *Pleonotoma* Miers (17), *Pyrostegia* C. Presl (2), *Stizophyllum* Miers (3), *Tanaecium* Sw. (17), *Tynanthus* Miers (15), and *Xylophragma* Sprague (7). Several genera are here circumscribed differently from previous classifications, in particular *Memora* Miers and *Sampaiella* J. C. Gomes are synonymized with *Adenocalymma*; *Distictella* Kuntze, *Distictis* Mart. ex Meisn., *Glaziova* Bureau, *Pithecoctenium* Mart. ex DC., and *Urbanolophium* Melch. are synonymized with *Amphilophium*; *Cydista* Miers, *Clytostoma* Miers ex Bureau, *Macranthisiphon* Bureau ex K. Schum., *Mussatia* Bureau ex Baill., *Phryganocydia* Mart. ex Bureau, *Potamoganos* Sandwith, *Roentgenia* Urb., and *Saritaea* Dugand are synonymized with *Bignonia*; *Macfadyena* A. DC., *Melloa* Bureau, and *Parabignonia* Bureau ex K. Schum. are synonymized with *Dolichandra*; *Arrabidaea* DC. is synonymized with *Fridericia*; *Gardnerodoxa* Sandwith is synonymized with *Neojobertia*; *Leucocalantha* Barb. Rodr. is synonymized with *Pachyptera*; and *Ceratophytum* Pittier, *Periarrabidaea* A. Samp., *Paragonia* Bureau, *Pseudocatalpa* A. H. Gentry, and *Spathicalyx* J. C. Gomes are synonymized with *Tanaecium*. The genera *Adenocalymma*, *Amphilophium*, *Fridericia*, *Dolichandra*, and *Tanaecium* are formally emended here as to diagnosis and circumscription. A natural key, complete morphological descriptions, and illustrations characterize the accepted genera, and full generic synonymy and a catalogue of their component species summarize their basic nomenclature and geographic range. Three new names are published: *B. neouliginosa* L. G. Lohmann replaces *Phryganocydia uliginosa* Dugand; *B. neoheterophylla* L. G. Lohmann replaces *Cydista heterophylla* Seibert; and *Tanaecium neobrasiliense* L. G. Lohmann replaces *Sanhilaria brasiliensis* Baill. Thirty-two generic names are newly synonymized, and 144 new nomenclatural combinations are made. A lectotype is designated for one genus, *Periarrabidaea* A. Samp., and 78 species names. One species name is neotypified, *Memora campicola* Pilg. (≡ *Adenocalymma campicola* (Pilg.) L. G. Lohmann).

Key words: Neotropical flora, Lamiales, Bignoniaceae, Bignonieae, *Adenocalymma*, *Amphilophium*, *Anemopaegma*, *Arrabidaea*, *Bignonia*, *Dolichandra*, *Fridericia*, *Tanaecium*.

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"Un jour viendra peut-être où quelques groupes naturels cesseront de s'accroître par les recherches même les plus intrépides et les plus persévérantes . . . mais, en attendant ce jour, dont l'aurore est lointaine, les travaux taxonomiques [dans la famille des Bignoniacées] conserveront un caractère provisoire . . ."

—Bureau (1864: 7, Monographie des Bignoniacées)

The tribe Bignonieae Dumort. (Bignoniaceae, Order Lamiales; APG, 2003) includes at least 393 species and is the largest tribe in the Bignoniaceae (Olmstead et al., 2009). The tribe includes both lianas and shrubs, and constitutes the most diverse and abundant clade of lianas in tropical New World lowland forests (Gentry, 1986). The tribe Bignonieae is exclusively American and most of its species are tropical, with a center of diversity in Brazil (Gentry, 1980); only three species are found in warm temperate North America: the native species *Bignonia capreolata* L., and the introduced species *Dolichandra unguis-cati* (L.) L. G. Lohmann (Manning, 2000) and *Amphilophium buccinatorium* (DC.) L. G. Lohmann. The tribe constitutes a well-supported monophyletic lineage within the Bignoniaceae (Spangler & Olmstead, 1999; Olmstead et al., 2009), which is sister to a clade composed of members of the tribes Catalpeae and Oroxyleae plus members of the Tabebuia Alliance and the Paleotropical Clade (Olmstead et al., 2009).

All members of tribe Bignonieae are woody, and most are lianas that climb using tendrils. Some genera also include shrubby species that grow in open dry vegetation such as the Brazilian cerrados and the Paraguayan, Bolivian, and Argentinian savannas. The leaves are opposite and compound, usually 3-foliolate, with the terminal leaflet often replaced by a tendril that is simple to multifid (Sousa-Baena et al., 2013, 2014). Less often, 1-foliolate, 5-foliolate, biternately compound, and biternately pinnate leaves are also found. Although Bignonieae lack stipules, the prophylls of the axillary buds are frequently well developed and stipule-like, and have sometimes been referred to as pseudostipules (e.g., Gentry, 1980). The stems of most species have anomalous secondary growth, with the phloem developing in four to 32 discontinuous wedges as seen in cross-section instead of the usual continuous ring of phloem found in other Bignoniaceae (Santos, 1995). This distinctive secondary growth results from failure of portions of the cambium to produce secondary xylem, which may give higher stem flexibility to the climbers (Atchley, 1976; Caballé, 1993; Pace et al., 2009, 2011). The twigs and young branches are cylindrical, tetragonal, or hexagonal in cross-section, and frequently have glands or extrafloral nectaries (EFNs) in the interpetiolar region. These EFNs are thought to be associated with herbivore defense (Gentry, 1974a; Lohmann, 2004; Nogueira et al., 2012a, 2012b). Mites housed in the domatia found in the axils of the secondary veins on the undersurfaces of the leaflets are also thought to play important roles in herbivore defense (Silva-Gomes, 2009).

The species of this tribe are noted for their showy flowers that are associated with a wide array of animal pollinators: bees, wasps, butterflies, hawkmoths, hummingbirds, and bats (Gentry, 1974a; Lohmann, 2004; Alcantara & Lohmann, 2010, 2011). The flowers are usually borne in terminal or axillary cymes, thyrses, and racemes, or less commonly in fascicles. The calyx is usually cupular, and frequently bears conspicuous glands of various shapes, sizes, densities, and distributions. These glands secrete sugar that attracts ants, which in turn protects the flowers from hummingbirds or xylocopid bees that will puncture the base of the corolla tube just above the calyx to steal nectar without pollinating the flower (Gentry, 1974a). The flowers are variously colored, including white, cream, yellow, orange, pink, purple, red, and blue. The corollas are 5-lobed, gamopetalous, and typically infundibuliform or occasionally tubular in form. The androecium consists of four didynamous stamens plus a small staminode, except in one species of *Tanaecium* Sw., *T. caudiculatum* (Standl.) L. G. Lohmann, which has two stamens and no staminodes. The gynoecium is composed of a bilocular superior ovary with axile placentation, an elongated style, and a bilamellate stigma. The ovary is typically surrounded by a conspicuous nectariferous disk, which offers rewards for pollinators (Gentry, 1978); occasionally the nectary is absent and mimetic pollination strategies are hypothesized (Heinrich & Raven, 1972; Umaña et al., 2011). The ovules are numerous, and are borne in one or more series on each placenta. The fruits are septicidal capsules of varied shape, size, and texture, and usually split at maturity into two valves. The seeds have a reduced endosperm and are typically winged and wind-dispersed, or sometimes corky and water-dispersed (Gentry, 1983b; Fischer et al., 2004; Lohmann, 2006).

Classification and postulation of species relationships in the past have been based on morphology, which is widely variable in this group and thus has supported a large number of different generic circumscriptions. Molecular data now provide additional evidence to discern relationships among the

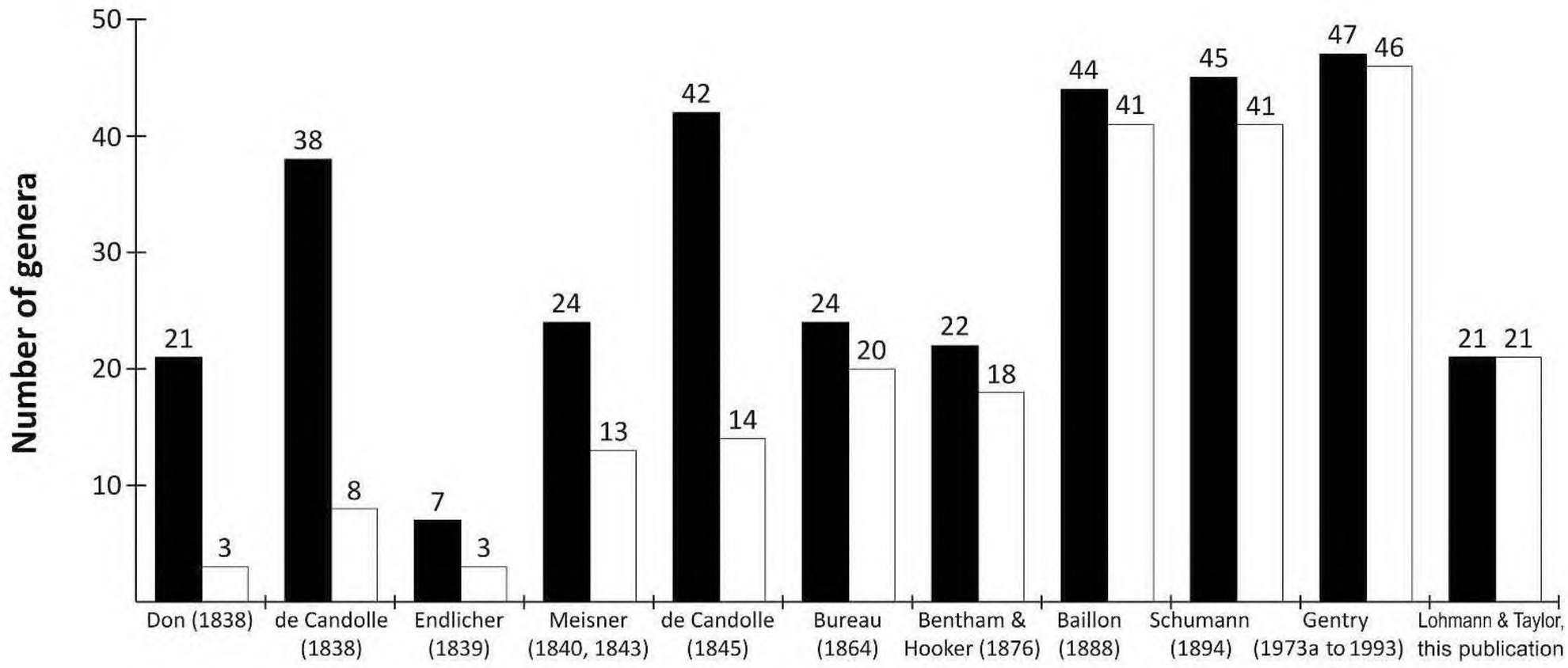


Figure 1. Number of Bignonieae genera in the different classification systems. Black bars indicate the total number of genera included under Bignonieae by that author; white bars indicate the total number of those genera that are still included in the tribe as either accepted names or synonyms.

taxa of this group (Lohmann, 2006), allowing for the identification of genus-level monophyletic groupings that are supported by key morphological characters. Here this new information is integrated with taxonomic studies of the species of this tribe to compile a new generic classification of the Bignonieae, a morphological characterization of these genera, and a list of the currently accepted species in the tribe. This present work relies significantly on the study materials and previous works, published and unpublished, of A. H. Gentry† (1945–1993).

Taxonomic History of Bignonieae

Bignonia L. was the first genus named in this family (Linnaeus, 1753). Jacquin (1963) subsequently treated the genus for the Caribbean region, while Aublet (1775) treated it for French Guiana. Later Jussieu (1789) described the ordo (equivalent there to family; McNeill et al., 2006, Art. 18.2) Bignones, which he divided into three numbered groups on the basis of habit and fruit dehiscence. Several subsequent authors described new species, new genera, and new morphology (Vahl, 1798; Willdenow, 1800 [1801]; Brown, 1810; Kunth, 1818, 1819; Vellozo, 1825 [1829]; Chamisso, 1832), but none of these treatments presented revised classifications between the family and genus level. Gentry (1980) and Spangler and Olmstead (1999) reviewed the classification of the family Bignoniaceae. The history of the classification of the tribe Bignonieae is outlined below, and the principal classifications are summarized in Table 1 and Figure 1.

The tribe Bignonieae was first recognized by Dumortier (1829: 23), as "Trib. 3. Bignoniaceae" in the family Rhinanthaceae. Dumortier clearly labeled his Rhinanthaceae a family and the group he there called Bignoniaceae a tribe, therefore the rank of his name is clear and its spelling must be corrected to Bignonieae (McNeill et al., 2006, Art. 19.6). Dumortier included in this tribe the same genera as Jussieu's family Bignoniaceae, but Jussieu's and Dumortier's names were published at different ranks and thus are distinct nomenclaturally. Dumortier's tribe Bignonieae is today classified in a different family—Bignoniaceae instead of Rhinanthaceae—and has a different circumscription, but these changes do not affect its valid publication. More specifically, Dumortier included in the tribe all genera with what he called an indistinct placentation type, with the seeds attached to the external borders of the placenta: *Bignonia*, *Tecoma* Juss., *Spathodea* P. Beauv., *Catalpa* Scop., *Chilopsis* D. Don, *Millingtonia* L. f., *Jacaranda* Juss., *Amphilophium* Kunth., *Eccremocarpus* Ruiz & Pav., and *Fieldia* A. Cunn. These genera are a heterogeneous assemblage today variously included in the family Gesneriaceae (*Fieldia*) and in the Bignoniaceae tribes Jacarandeae, Tourretieae, Tecomeae, Oroxyleae, and Bignonieae and also the Paleotropical Clade of Olmstead et al. (2009).

Bojer (1837) next studied the tribe Bignonieae, and placed in it all Bignoniaceae with a bilocular silique fruit and winged seeds. Bojer's treatment was restricted to the island of Mauritius, and he included here only *Bignonia*, *Catalpa*, and *Spathodea*, which are all currently included in the family Bignoniaceae but variously classified in the tribes Bignonieae and Catalpeae and the Paleotropical Clade of Olmstead et al. (2009), respectively. Bojer first used the degree of calyx lobing as a generic character, and this has

Table 1. Comprehensive treatments of Bignonieae. Genera marked with a ✔ were included in Bignonieae as either accepted names or synonyms. See text for detailed discussion and nomenclature.

Don (1838)	de Candolle (1838)	Endlicher (1839)	Meisner (1840, 1843)
Tribe Bignonieae	Tribe Bignonieae	Tribe Eubignonieae	Tribe Eubignoniées
I.	Subtribe I. Eubignonieae	(= Tribe Bignonieae)	(= Tribe Bignonieae)
✔*Amphilophium*	(= Subtribe Bignoninae)	✔*Amphilophium*	Division Monostictides
Asianthus	✔*Amphilophium*	*Asianthus*	✔*Arrabidaea*
✔*Bignonia*	*Argylia*	✔*Bignonia*	(= *Fridericia*)
Chilopsis	✔*Arrabidaea*	*Calosanthes*	*Asianthus*
Delostoma	(= *Fridericia*)	*Delostoma*	✔*Bignonia*
Ferdinandusa	*Asianthus*	✔*Haplolophium*	*Calosanthes*
✔*Fridericia*	✔*Bignonia*	(= *Amphilophium*)	✔*Cuspidaria*
Jacaranda	*Calosanthes*	*Millingtonia*	*Ferdinandusa*
Oxera	✔*Cuspidaria*		✔*Haplolophium*
Spathodea	*Delostoma*		(= *Amphilophium*)
Stenolobium	✔*Haplolophium*		✔*Lundia*
Tecoma	(= *Amphilophium*)		✔*Mansoa*
Zeyheria	✔*Lundia*		*Millingtonia*
II.	✔*Mansoa*		*Oxera*
Calosanthes	*Millingtonia*		*Pachyptera*
Platycarpum	*Stereospermum*		*Peltospermum*
III.	Subtribe II. Catalpeae		*Psilogyne*
Argylia	(= Subtribe Catalpinae)		*Schrebera*
Incarvillea	*Catalpa*		*Sickingia*
Millingtonia	*Chilopsis*		*Wightia*
Wightia	*Eccremocarpus*		Division Pleiostictides
IV.	✔*Fridericia*		✔*Adenocalymma*
Catalpa	*Heterophragma*		✔*Amphilophium*
Schrebera	*Jacaranda*		✔*Anemopaegma*
	Neowedia		*Cybistax*
	Pajanelia		*Delostoma*
	Pawllonia		✔*Distictis*
	Spathodea		(= *Amphilophium*)
	Tabebuia		✔*Pithecoctenium*
	Tecoma		(= *Amphilophium*)
	Tourrettia		
	Zeyheria		
	Subtribe III. Gelsemieae		
	(= Subtribe Gelseminae)		
	Bravasia		
	Esterhazya		
	Gelsemium		
	Holoregmia		
	Peltospermum		
	Platycarpum		
	Psilogyne		
	Rhigozum		
	Schrebera		
	Trigonocarpus		
	Wightia		

de Candolle (1845)	Bureau (1864)	Bentham (1876)	Baillon (1888)
Tribe Bignonieae	Groupe I.	Tribe Bignonieae	Série des Bignones
Subtribe Eubignonieae	(= Tribe Bignonieae)	Division Monostictides	(= Tribe Bignonieae)
(= Subtribe Bignoninae)	✔*Adenocalymma*	✔*Adenocalymma*	✔*Adenocalymma*
Division Monostictides	✔*Amphilophium*	✔*Anemopaegma*	✔*Amphilophium*
✔*Anemopaegma*	✔*Anemopaegma*	✔*Arrabidaea*	✔*Anemopaegma*
✔*Arrabidaea*	✔*Anisostichus*	(= *Fridericia*)	✔*Arrabidaea*
(= *Fridericia*)	(= *Bignonia*)	✔*Bignonia*	(= *Fridericia*)
Asianthus	✔*Arrabidaea*	✔*Cuspidaria*	✔*Bignonia*

Table 1. Continued.

de Candolle (1845)	Bureau (1864)	Bentham (1876)	Baillon (1888)
✔*Bignonia*	(= *Fridericia*)	✔*Fridericia*	✔*Callichlamys*
Calosanthes	✔*Bignonia*	✔*Lundia*	✔*Clytostoma*
✔*Cuspidaria*	*Calosanthes*	✔*Macfadyena*	(= *Bignonia*)
✔*Distictis*	✔*Callichlamys*	(= *Dolichandra*)	✔*Cremastus*
(= *Amphilophium*)	✔*Cuspidaria*	✔*Melloa*	(= *Cuspidaria*)
✔*Fridericia*	✔*Distictis*	(= *Dolichandra*)	✔*Cuspidaria*
✔*Haplolophium*	(= *Amphilophium*)	✔*Saldanhaea*	✔*Cydista* (= *Bignonia*)
(= *Amphilophium*)	✔*Fridericia*	(= *Cuspidaria*)	✔*Distictis*
✔*Lundia*	✔*Haplolophium*	✔*Tynanthus*	(= *Amphilophium*)
✔*Macfadyena*	(= *Amphilophium*)	Division Pleostictides	✔*Doxantha*
(= *Dolichandra*)	*Leguminaria*	✔*Amphilophium*	(= *Dolichandra*)
✔*Mansoa*	✔*Lundia*	✔*Callichlamys*	✔*Fridericia*
Millingtonia	✔*Macfadyena*	✔*Distictis*	✔*Glaziovia*
✔*Pachyptera*	(= *Dolichandra*)	(= *Amphilophium*)	(= *Amphilophium*)
Division Pleostictides	✔*Macrodiscus*	✔*Glaziovia*	✔*Haplolophium*
✔*Adenocalymma*	(= *Amphilophium*)	(= *Amphilophium*)	(= *Amphilophium*)
✔*Amphilophium*	✔*Mansoa*	✔*Haplolophium*	✔*Levya* (= *Bignonia*)
Cybistax	*Microdiscus*	(= *Amphilophium*)	✔*Lundia*
Delostoma	*Millingtonia*	*Haussmannia*	✔*Macfadyena*
✔*Pithecoctenium*	✔*Pachyptera*	*Millingtonia*	(= *Dolichandra*)
(= *Amphilophium*)	✔*Pithecoctenium*	*Nyctocalos*	✔*Macrodiscus*
Subtribe Catalpeae	(= *Amphilophium*)	*Oroxylum*	(= *Amphilophium*)
(= Subtribe Catalpinae)	✔*Pyrostegia*	✔*Pithecoctenium*	✔*Mansoa*
Division Monostictdes	✔*Schizopsis*	(= *Amphilophium*)	✔*Martinella*
Argylia	(= *Tynanthus*)	✔*Tanaecium*	✔*Melloa* (= *Dolichandra*)
Catalpa	✔*Tanaecium*		✔*Memora*
Catophractes			(= *Adenocalymma*)
Chilopsis			*Millingtonia*
Craterotecoma			✔*Mussatia* (= *Bignonia*)
Heterophragma			✔*Neojobertia*
Jacaranda			✔*Neomacfadyena*
Pajanella			(= *Fridericia*)
Platycarpum			*Nyctocalos*
Rhigozum			*Oroxylum*
Spathodea			✔*Paragonia*
Stereospermum			(= *Tanaecium*)
Tabebuia			✔*Paramansoa*
Tecoma			(= *Fridericia*)
Tourrettia			✔*Perianthomega*
Zeyheria			✔*Petastoma* (= *Cuspidaria*)
Division Pleiostictides			✔*Phaedranthus*
Sparattosperma			(= *Amphilophium*)
Subtribe Incarvilleae			✔*Phryganocydia* (= *Bignonia*)
(= Subtribe Incarvillinae)			✔*Pithecoctenium*
Amphicone			(= *Amphilophium*)
Incarvillea			✔*Pleonotoma*
Subtribe Eccremocarpeae			✔*Pyrostegia*
(= Subtribe Eccremocarpinae)			✔*Saldanhaea*
Bravaisia			(= *Cuspidaria*)
Dipterosperma			✔*Sanhilaria*
Eccremocarpus			(= *Tanaecium*)
Pteropodium			✔*Setilobus*
			(= *Cuspidaria*)
			✔*Stizophyllum*
			✔*Tanaecium*
			✔*Tynanthus*

Table 1. Continued.

Schumann (1894)	Gentry (1973a to 1993, unpubl.)	Lohmann & Taylor, this publication
Tribe Bignonieae	Tribe Bignonieae	Tribe Bignonieae
✔*Adenocalymma*	✔Adenocalymma	✔*Adenocalymma*
✔*Amphilophium*	✔*Amphilophium*	✔*Amphilophium*
✔*Anemopaegma*	✔*Anemopaegma*	✔*Anemopaegma*
✔*Arrabidaea*	✔*Arrabidaea*	✔*Bignonia*
(= *Fridericia*)	(= *Fridericia*)	✔*Callichlamys*
✔*Bignonia*	✔*Bignonia*	✔*Cuspidaria*
✔*Callichlamys*	✔*Callichlamys*	✔*Dolichandra*
✔*Clytostoma* (= *Bignonia*)	✔*Ceratophytum*	✔*Fridericia*
✔*Cremastus* (= *Cuspidaria*)	(= *Tanaecium*)	✔*Lundia*
✔*Cuspidaria*	✔*Clytostoma* (= *Bignonia*)	✔*Manaosella*
✔*Cydista* (= *Bignonia*)	✔*Cuspidaria*	✔*Mansoa*
✔*Distictis*	✔*Cydista* (= *Bignonia*)	✔*Martinella*
(= *Amphilophium*)	✔*Distictella*	✔*Neojobertia*
✔*Doxantha*	(= *Amphilophium*)	✔*Tanaecium*
✔*Fridericia*	✔*Distictis*	✔*Pachyptera*
✔*Glaziovia*	(= *Amphilophium*)	✔*Perianthomega*
(= *Amphilophium*)	✔*Dolichandra*	✔*Pleonotoma*
✔*Haplolophium*	✔*Fridericia*	✔*Pyrostegia*
(= *Amphilophium*)	✔*Gardnerodoxa*	✔*Stizophyllum*
Haussmannia	(= *Neojobertia*)	✔*Tynanthus*
✔*Levya* (= *Bignonia*)	✔*Glaziovia*	✔*Xylophragma*
✔*Lundia*	(= *Amphilophium*)	
✔*Macfadyena*	✔*Haplolophium*	
(= *Dolichandra*)	(= *Amphilophium*)	
✔*Macranthisiphon*	✔*Leucocalantha*	
(= *Bignonia*)	(= *Pachyptera*)	
✔*Macrodiscus*	✔*Lundia*	
(= *Amphilophium*)	✔*Macfadyena*	
✔*Mansoa*	(= *Dolichandra*)	
✔*Martinella*	✔*Macranthisiphon*	
✔*Melloa*	(= *Bignonia*)	
(= *Dolichandra*)	✔*Manaosella*	
✔*Memora*	✔*Mansoa*	
(= *Adenocalymna*)	✔*Martinella*	
Millingtonia	✔*Melloa* (= *Dolichandra*)	
✔*Mussatia* (= *Bignonia*)	✔*Memora*	
✔*Neojobertia*	(= *Adenocalymna*)	
✔*Neomacfadyena*	✔*Mussatia* (= *Bignonia*)	
(= *Fridericia*)	✔*Neojobertia*	
Nyctocalos	✔*Parabignonia*	
Oroxylum	(= *Dolichandra*)	
✔*Paragonia*	✔*Paragonia*	
(= *Tanaecium*)	(= *Tanaecium*)	
✔*Paramansoa*	✔*Periarrabidaea*	
(= *Fridericia*)	(= *Tanaecium*)	
✔*Perianthomega*	✔*Phryganocydia*	
✔*Phaedranthus*	(= *Bignonia*)	
(= *Amphilophium*)	✔*Piriadacus*	
✔*Phryganocydia*	(= *Fridericia*)	
(= *Bignonia*)	✔*Pithecoctenium*	
✔*Pithecoctenium*	(= *Amphilophium*)	
(= *Amphilophium*)	✔*Pleonotoma*	
✔*Pleonotoma*	✔*Potamoganos*	
✔*Pyrostegia*	(= *Bignonia*)	
✔*Saldanhaea*	✔*Pseudocatalpa*	
(= *Cuspidaria*)	(= *Tanaecium*)	

Table 1. Continued.

Schumann (1894)	Gentry (1973a to 1993, unpubl.)
✔*Sanhilaria* (= *Tanaecium*)	✔*Pyrostegia*
✔*Setilobus* (= *Tynanthus*)	✔*Roentgenia* (= *Bignonia*)
✔*Stizophyllum*	✔*Saritaea* (= *Bignonia*)
✔*Tanaecium*	✔*Spathicalyx* (= *Tanaecium*)
✔*Tynanthus*	✔*Stizophyllum*
✔*Xylophragma*	✔*Tanaecium*
	✔*Tynanthus*
	✔*Xylophragma*

proven to be a useful indicator of some generic relationships in Bignonieae.

The first comprehensive treatment of the tribe Bignonieae was by Don (1838). His circumscription of this tribe, like that of Bojer, was broad and included all the members of the family Bignoniaceae with a 2-valved capsule and winged seeds. However, these are common characters in the family, which led to the recognition of a systematically heterogeneous Bignonieae. Only three of the genera that Don included in his tribe Bignonieae (*Bignonia*, *Amphilophium*, and *Fridericia* Mart.) are retained in this tribe today; his other 18 genera are now variously classified in other Bignoniaceae tribes, the Lamiaceae (*Oxera* Labill.), the Scrophulariaceae (*Wightia* Wall.), and the Rubiaceae (*Ferdinandusa* Pohl). Don added corolla, stamen, and fruit characters to his generic diagnoses, and separated the genera of the tribe Bignonieae into numbered but unranked groups based on number of fertile stamens and staminodes.

Augustin Pyramus de Candolle (1838) presented a comprehensive synoptic treatment of the family Bignoniaceae, with 336 species and 38 genera included in the tribe Bignonieae and the remaining members of this family placed in the tribe Crescentieae. He followed previous authors in including in the tribe Bignonieae all the members of this family with dehiscent fruits and winged seeds. Here he recognized three subtribes, Eubignoniées (i.e., Bignoniinae), Catalpées (i.e., Catalpinae), and Gelsemiées (i.e., Gelsemiinae), plus a group of nine monotypic genera separated as genera non satis nota seu anomala (i.e., incompletely known or unusual genera). De Candolle was the first to give importance to capsule dehiscence, whether loculicidal, septicidal, or indehiscent, which he used to characterize his subtribes. Molecular phylogenetic data have indicated that capsule dehiscence types represent morphological synapomorphies of clades and are indeed informative characters for delimiting tribes within the family Bignoniaceae (Spangler & Olmstead, 1999; Olmstead et al., 2009). De Candolle's subtribe Bignoniinae included seven genera that are today included in tribe Bignonieae, and six genera that are now included in tribe Tecomeae or in the Paleotropical Clade of Olmstead et al. (2009). *Fridericia*, now classified in tribe Bignonieae, was separated in de Candolle's subtribe Catalpinae, which also included members of several other modern Bignoniaceae tribes as well as of the families Acanthaceae and Paulowniaceae. De Candolle's subtribe Gelsemiinae and the genera non satis nota seu anomala did not include any members of tribe Bignonieae as currently circumscribed.

Endlicher's (1839) treatment of the family was restricted to the generic level and did not closely follow previous taxonomies. He divided the family Bignoniaceae into five subordos (equivalent to subfamilies; McNeill et al., 2006, Art. 19.2): Sesameae (i.e., Sesamoideae; two genera), Eccremocarpeae (i.e., Eccremocarpoideae; three genera, including *Fridericia*), Incarvilleae (i.e., Incarvilleoideae; two genera), Tourretieae (i.e., Tourretioideae; one genus), and Bignonieae (i.e., Bignonioideae; 14 genera). He characterized the subfamily Bignonioideae in the same way that previous authors characterized the tribe Bignonieae, by a bilocular septicidal capsule and usually winged seeds, together with a new character, hypogeal seedling elongation, which was also found in his subfamily Eccremocarpoideae. Endlicher recognized three tribes within his Bignonioideae, Tribe 1. Argylieae, Tribe 2. Tecomeae, and Tribe 3. Eubignonieae (i.e., Bignonieae). His tribe Bignonieae corresponded to de Candolle's (1838) subtribe Bignoniinae and was similarly characterized by a septicidal capsule and winged seeds. It included seven genera, only three of which are currently included in Bignonieae (*Amphilophium*, *Bignonia*, and *Haplolophium* Cham.). Endlicher's tribe Tecomeae was generally equivalent to de Candolle's subtribe Catalpinae, both of which were characterized by septicidal capsules and winged

seeds and did not include any genera of today's tribe Bignonieae. Endlicher's Argylieae was monogeneric, had no equivalent in de Candolle's classification, and did not include any genus of today's Bignonieae; it was characterized by a septicidal capsule and unwinged seeds.

Meisner (1840, 1843; sometimes also spelled Meissner, Stafleu & Cowan, 1981) recognized two subordos (equivalent to subfamilies) of Bignoniaceae, Bignonieae (i.e., Bignonioideae) and Crescentineae (i.e., Crescentioideae). He followed Endlicher (1839) in recognizing the subfamily Bignonioideae, and de Candolle (1838) in dividing this into the tribes Eubignoniées (i.e., Bignonieae), Catalpées (i.e., Catalpeae), and Gelsemiées (i.e., Gelsemieae). A novelty of Meisner's system was the division of tribes Bignonieae and Catalpeae into two further groups each, similarly named in each tribe. These were called Monostictides and Pleiostictides, and were equivalent to subtribes (however, because a name can only be used once, some of these subtribe names are illegitimate). These were characterized by the number of seed series on each placenta, one versus more than one, respectively. Meisner's circumscription of Bignonieae was much broader than that of today, and included various members of tribe Bignonieae, other Bignoniaceae tribes and subtribes, Rubiaceae (*Ferdinandusa* Pohl), Apocynaceae (*Peltospermum* DC., now included in *Aspidosperma* Mart. & Zucc.), and Lamiaceae (*Psilogyne* DC., now included in *Vitex* L.). Meisner followed Endlicher in excluding *Fridericia*, today included in the tribe Bignonieae, from this tribe based on fruit morphology. Under Meisner's system, *Fridericia* was included in tribe Catalpeae, subtribe Monostictides.

Augustin Pyramus de Candolle prepared the next treatment of the family Bignoniaceae, based on the earlier family monograph (de Candolle, 1838) but now expanded into the sole work ever to treat all known genera and species of the family with full descriptions (de Candolle, 1845). This monograph was edited and modified before publication by his son, Alphonse de Candolle, who clearly indicated his own additions or changes from his father's version. Here the two basic subdivisions of the family were maintained, with 492 species in the broadly circumscribed tribe Bignonieae, 173 of which were still classified in the highly heterogeneous *Bignonia*. However, in this new classification the infratribal divisions were changed. The subtribes Bignoniinae and Catalpinae were retained, but the Gelsemiinae was no longer recognized, while Endlicher's (1839) subfamilies Incarvilleoideae and Eccremocarpoideae were here treated as subtribes Incarvilleae (i.e., Incarvilleinae) and Eccremocarpeae (i.e., Eccremocarpinae). Capsule dehiscence was still important for distinguishing the subtribes. The Catalpinae, Incarvilleinae, and Eccremocarpinae were all characterized by loculicidal capsules, and included a heterogenerous group of taxa that are today included variously in the Bignoniaceae tribes Tecomeae, Catalpeae, and Tourretieae and the Tabebuia Alliance and the Paleotropical Clade of Olmstead et al. (2009), in Rubiaceae (*Platycarpum* Bonpl.), and in Acanthaceae (*Bravaisia* DC.). His subtribe Bignoniinae, on the other hand, was characterized by a septicidal capsule and is similar to the tribe Bignonieae as currently cirumscribed. This classification also followed Meisner (1840, 1843) in dividing Bignoniinae and Catalpinae each into groups called Monostictides and Pleiostictides, but differed from Meisner in transferring *Anemopaegma* Mart. ex Meisn. and *Distictis* Mart. ex Meisn. from Pleiostictides to Monostictides. This treatment also adopted a significantly narrower circumscription of *Bignonia*, with 191 species here excluded from this genus and placed variously in *Cuspidaria* DC., *Fridericia* Mart., *Lundia* DC., *Mansoa* DC., *Heterophragma* DC., *Peltospermum* DC., and *Boutonia* DC. However, tribe Bignonieae remained highly heterogeneous in this classification, with only 14 of de Candolle's 42 genera still included today in this tribe.

Bureau (1864: 23) considered the higher-level classification of de Candolle (1845) "more simple and more natural" than that of Endlicher because of its fewer major groupings. However, Bureau did not accept this classification, but instead divided the family into 15 major groups that are equivalent to today's tribes but were numbered rather than named. For each group Bureau chose a type or exemplar genus that he used to characterize the group as a whole. The type genus was chosen to have the highest number of characters in common with other members of the group and provide the best generalization of the group. Bureau's Group I, exemplified by *Arrabidaea* and characterized by a septicidal capsule, corresponds to today's Bignonieae. Bureau's circumscription of Bignonieae was much narrower than previously, and much more similar to today's circumscription with 20 of his 24 genera still classified in this tribe. Only one genus of today's Bignonieae, *Dolichandra* Cham., was excluded from Bureau's Group I and included in his Group II instead. Bureau's system was also novel in its use of combinations of characters to diagnose the groups, in particular septum position, number of fertile stamens, and number of ovary locules. Bureau had a relatively

narrow generic concept and split several of the existing genera.

Bentham's (1876) treatment of the Bignoniaceae did not closely follow previous classifications. The family was divided into four tribes: Bignonieae, Tecomeae, Jacarandeae, and Crescentieae. Similarly to Bureau, he included in the tribe Bignonieae all the genera with septicidal capsules; of the 21 genera classified here, 15 were shared with Bureau's classification. Unlike Bureau but similarly to Meisner (1840, 1843) and de Candolle (1845), Bentham divided the tribe Bignonieae into the subgroups Monostictides and Pleiostictides. However, *Adenocalymma* was transferred into Monostictides, and *Haplolophium* into Pleiostictides. In addition, Bentham followed de Candolle in placing *Anemopaegma* under Monostictides, but followed Meisner (1840, 1843) in placing *Distictis* back into Pleiostictides. Bentham recognized much more broadly circumscribed genera than did Bureau and again included several species of *Arrabidaea* and a number of small genera (*Anisostichus* Miers, *Cremastus* Miers, *Cydista* Bureau, *Doxantha* Miers, *Panterpa* Miers, *Paragonia* Bureau, *Petastoma* Miers, *Phaedranthus* Miers, *Pleonotoma* Miers, *Pyrostegia* C. Presl, and *Stizophyllum* Miers) in *Bignonia*. He also synonymized some other genera, in particular *Craterotecoma* Mart. ex Meisn. with *Lundia*, *Dolichandra* with *Macfadyena* A. DC. and *Pachyptera* and *Memora* with *Adenocalymma*. This reduction in the number of genera perhaps reflected Bentham's concerns about memory and the number of genera that should be recognized (Stevens, 1997a, 1997b). His view in this was rejected by subsequent authors.

Baillon (1888) next presented a classification for this family, which differed from previous ones in recognizing a série des Bignones (i.e., tribe Bignonieae) without any subdivisions. He also rejected Bentham's (1876) broad genus circumscriptions, recognizing 13 genera that had been placed in synonymy and describing several new genera, notably *Martinella* Baill., *Neojobertia* Baill., *Neomacfadya* Baill., *Paramansoa* Baill., *Sanhilaria* Baill., and *Setilobus* Baill. In total, Baillon here recognized 44 genera in the tribe Bignonieae, of which 41 are still included in the tribe (as either accepted names or synonyms). However, he again placed *Dolichandra* in a different tribe, following Bureau (1864). Baillon cited exemplar species or sometimes listed component species for his new genera, but did not explicitly associate the new genus name with these species epithets. Therefore he did not publish valid new combinations for the species in his new genera (McNeill et al., 2006, Art. 33.1).

Schumann's (1894) treatment of the family Bignoniaceae for the *Natürlichen Pflanzenfamilien* presented the most recent comprehensive treatment until now for the tribe Bignonieae at the generic level, but he mostly did not detail the species. Schumann closely followed Baillon's (1888) tribal circumscriptions for this family, recognizing Bignonieae, Tecomeae, Eccremocarpeae, and Crescentieae, but included one additional tribe, the Tourretieae. He also followed Baillon's narrow generic delimitations. Schumann recognized 43 of the 44 genera recognized in the tribe Bignonieae by Baillon, synonymizing only *Petastoma*, and added two genera to it, *Macranthisiphon* Bureau ex K. Schum. and *Haussmannia* F. Muell. (= *Neosepicaea* Diels, currently classified in the tribe Oroxyleae). Also similarly to Baillon, no subdivisions were recognized within the tribe.

Contemporaneously with this family synopsis (Schumann, 1894) the two main specialists in this family collaborated to produce a complete floristic treatment of the Bignoniaceae for the *Flora Brasiliensis* (Bureau & Schumann, 1896). These two works followed the same family classification and generic circumscriptions. Schumann's (1894) family synopsis extensively referenced and included information from this flora, and in some cases validated new names used in the flora. The family synopsis is written in a way that suggests it may have originally been expected to be published after the flora (the nomenclatural aspects of this situation are discussed in more detail in the Taxonomic Treatment section below). Bureau and Schumann provided detailed descriptions of all 36 genera and 260 species of the tribe Bignonieae occurring in Brazil, and because Brazil is the center of diversity of Bignonieae their treatment remains a major reference for this group.

Since Bureau and Schumann's time several botanists have studied individual genera and/or produced comprehensive floras that have contributed significantly to understanding the tribe Bignonieae, but no work has addressed the tribe as a whole. By the 1900s, a narrow generic concept predominated among students of the Bignoniaceae and generic splitting became common. For example, Urban (1916) described *Pseudopaegma* Urb., *Roentgenia* Urb., and *Nestoria* Urb.; Melchior (1927) described *Urbanolophium* Melch.; Sampaio and Kuhlmann (1934) described *Pseudocalymma* A. Samp. & Kuhlm.; Dugand (1945) described *Saritaea* Dugand; Pichon (1946) described 11 new genera; and Gomes (1949, 1956) described *Sampaiella* J. C. Gomes, *Spathicalyx* J. C. Gomes, and *Kuhlmannia* J. C. Gomes. None of these new genera included more than two species, none was easily separable morphologi-

cally, and none is recognized in the present classification.

Sandwith published approximately 20 works between 1937 and 1974 that significantly influenced the systematics of Bignoniaceae and particularly of the tribe Bignonieae (see Brenan, 1966, for a review of Sandwith's publications), but he did not present a comprehensive treatment of the tribe. His works presented descriptions of individual new species, floristic inventories, nomenclatural adjustments, and some changes of generic circumscription. He described the new genus *Potamoganos* Sandwith (1937) and again recognized several other genera that had been synonymized (e.g., *Sideropogon* Pichon, *Saritaea*, and *Roentgenia*), but he also synonymized *Onohualcoa* Lundell with *Mansoa*, *Pseudopaegma* with *Anemopaegma*, *Sanhilaria* with *Paragonia*, and *Nestoria* and *Kuhlmannia* with *Pleonotoma*. Notably Sandwith significantly expanded the circumscription of *Arrabidaea* to include the previously recognized genera *Petastoma*, *Panterpa*, *Cremastus*, *Paramansoa*, *Scobinaria* Siebert, *Paracarpaea* (K. Schum.) Pichon, *Tetrastichella* Pichon, and *Sampaiella*.

Alwyn H. Gentry was the most recent major student of the family Bignoniaceae. He recognized eight tribes in this family, of which Bignonieae was the largest. The early heterogeneous circumscription of the tribe had been much improved by Bureau (1864), but it remained diagnosed by a single character, fruit septum position, until Gentry (1980) incorporated characters of habit, wood anatomy, and tendrils. This clarified its circumscription and allowed classification of a number of previously controversial taxa. Of the genera that were found in this present analysis to belong to the tribe Bignonieae, Gentry (1990, 1992c) excluded only *Perianthomega* Bureau ex Baill. By the time Gentry started his work, generic splitting had reached the point that the tribe Bignonieae had the lowest ratio of species to genera of any sizeable group of angiosperms (Gentry, 1973a). Gentry's circumscription of genera was based on newly studied morphological, anatomical, pollen and field data, representing a significant advance for the taxonomy of the family. He used a broader generic concept than that of recent authors, and decreased significantly the number of genera in the tribe by merging genera that were separated by characters he considered unreliable. Those unreliable characters included inflorescence branching pattern, degree of seed thickening, seed wing length, and seed pubescence (Gentry, 1973a, 1976, 1979). Gentry's contributions to knowledge of the tribe Bignonieae also extended to a much improved understanding of the distribution, floristics, and ecology of the species and genera (see Miller et al., 1996, for a review of Gentry's publications).

It is very unfortunate that Gentry was unable to produce a comprehensive classification and revision of the tribe before his untimely death. His work was well advanced by then, however, and his view of the classification of this tribe is inferred from his publications (in particular Gentry, 1973a, 1975, 1976, 1979, 1985, 1992b, 1992c, 1993) and referred to here as Gentry's system. In this classification 47 genera were recognized in the tribe Bignonieae (Table 1), of which 30 genera had three or fewer species, while *Adenocalymma*, *Anemopaegma*, *Arrabidaea*, and *Memora* Miers together had 250 species and comprised the majority of the species then recognized in the tribe. Gentry (1973a) himself noted that some of these genera were highly polymorphic and included such a wide range of morphological variation that their species sometimes lacked the supposed diagnostic features of the genus. Although Gentry did not present a full taxonomic treatment of the tribe Bignonieae, his Neotropical floristic treatments cover a wide geographic range and provide an essential detailing of the majority of Bignonieae taxa that forms the basis of the species-level classification here (Gentry, 1973b, 1977, 1982, 1983a, 1997). Additional taxonomic studies prepared with access to his unfinished works and specimen annotations present significant additional data for the tribe Bignonieae (Hauk, 1997, 1999, 2002; Pool, 2007a, 2007b, 2008, 2009).

A New Classification of Tribe Bignonieae

Here, a new, phylogenetically based classification is adopted, with the hypotheses of phylogenetic relationships explicitly formulated, the relationships among the taxa detailed, and the basis for the circumscriptions of genera spelled out. The classification of the tribe Bignonieae here differs from previous treatments in several ways, in particular the inclusion here of *Perianthomega* (in this following Baillon, 1888, and Schumann, 1894), the recognition of 21 rather than 47 genera, the synonymization of several well-known genera, and the separation here of the species formerly placed in the polyphyletic genus *Arrabidaea* (Lohmann, 2006) variously in *Fridericia*, *Cuspidaria*, and *Tanaecium*.

Not surprisingly, several of the genera recognized here based on molecular data have been previously accepted. For example, Bentham (1876) placed *Adenocalymma* and *Memora* in synonymy more than 100 years ago, and Gentry (1973a) separated them but agreed that they were closely related and may be considered a single genus. The affinities between

Phryganocydia Mart. ex Bureau, *Cydista*, *Clytostoma* Miers ex Bureau, *Roentgenia*, *Potamoganos*, and *Mussatia* Bureau ex Baill. were also noted before (Gentry, 1973a; Hauk, 1997, 2002); these are all here included in *Bignonia*. The subtribe Pithecocteniinae of Melchior (1927) included *Amphilophium*, *Distictella* Kuntze, *Haplolophium*, and *Pithecoctenium* Mart. ex Meisn., and together with *Distictis* and *Glaziova* these genera are here included within *Amphilophium*. The affinities among *Dolichandra*, *Macfadyena*, *Melloa*, and *Parabignonia* were emphasized by Santos (1995) on the basis of wood anatomy, and by Gentry and Tomb (1979) on the basis of pollen characters; these are here all included in *Dolichandra*. Gentry (1973a) also suggested that *Tanaecium*, *Paragonia*, and *Ceratophytum* were closely related, and these are all included here in *Tanaecium*.

While several previously suspected relationships were corroborated by molecular data (Lohmann, 2006), the analyses based on that data also recovered some previously unsuspected relationships. In particular the close relationship between *Sampaiella* and *Adenocalymma*, the sister relationship between *Leucocalantha aromatica* Barb. Rodr. and *Mansoa kerere* (Aubl.) A. H. Gentry, the sister relationship between *Neojobertia* and *Gardnerodoxa*, the close relationship of *Tanaecium nocturnum* (Barb. Rodr.) Bureau & K. Schum. to *Bignonia*, and the close relationship among *Arrabidaea revillae* A. H. Gentry, *Arrabidaea selloi* (Spreng.) Sandwith, and the *Tanaecium* clade were previously unrecognized. When these relationships were studied, several morphological characters were found that also unite those groups. In addition, the overall relationships among genera were completely unclear until the molecular phylogenetic data became available (Lohmann, 2006).

Because the classification presented below is based on a robust molecular phylogenetic analysis backed by morphological evidence, it is expected to be more stable than previous ones. Stability of classification depends on the principle that there are only rarely reasons for dividing a genus into two or more monophyletic genera if its own monophyletic status remains unquestioned, even if smaller monophyletic genera can be recognized by morphological synapomorphies (Stevens, 2001 onwards). This principle is incorporated into the classification adopted here. The genera most deeply changed here in diagnosis and circumscription are *Adenocalymma*, *Amphilophium*, *Dolichandra*, *Fridericia*, and *Tanaecium*. The changes in all of these meet the criterion of considerable alteration (McNeill et al., 2006, Art. 47, Rec. 47A) and are here designated as emendavit (i.e., emended). The diagnosis of *Bignonia* is also changed here from recent usage; however, the characterization of this genus has varied so widely and continually since its original description that there is no stable reference circumscription against which to measure the change here in the classification, and this genus is not formally designated as emended here.

The phylogeny reconstruction on which this classification is based is detailed elsewhere (Lohmann, 2006). In brief, first morphologically similar groups of species linked by putative synapomorphies were identified. Each of these morphological groups was sampled in the phylogenetic study and represented by two or three species; overall about a third of the species currently recognized in the tribe (120 of 393 species) were included in the analysis. Morphologically similar species were studied to ensure that morphological uniformity did not hide molecular variation. Species were sampled from all but one (*Macranthisiphon* Bureau ex K. Schum.) of the 47 genera of the tribe Bignonieae recognized in Gentry's system (Table 2) plus *Perianthomega*, which was previously included in Bignonieae by Baillon (1888) and Schumann (1894) but separated in the tribe Tecomeae by Gentry (1992c). For each species included in the analysis, sequences of the fourth intron of one of the nuclear genes for phosphoenolpyruvate carboxylase (*Pep*C) and the chloroplast gene NADH dehydrogenase subunit 6 (*ndh*F) were obtained, and a morphological study was conducted. The combined molecular data produced a robust phylogeny (Lohmann, 2006), which for clarity is shown here in a simplified tree (Fig. 2). This tree shows only the significant nodes, which are lettered, and the clades that are recognized here with the generic names used.

The issue of which clades should be recognized in a classification is controversial. The classification here follows the principle used by APG (1998: 531) that "classification is not [simply] a matter of grouping according to the principle of monophyly, but it is also a matter of communication." The classification presented here aims to show phylogenetic relationships among taxa and patterns of character evolution. Accordingly, here a clade is regarded as a genus whenever it is a well-supported monophyletic group that can be recognized by one or more morphological synapomorphies. Therefore when small monophyletic genera that have been previously recognized lack diagnostic morphological characters, are too small to be informative about phylogenetic relationships (i.e., only include a few species), or exclude species with similar characters, they are

included within a larger genus circumscription that satisfies the principle of generic recognition used here.

Morphology

A comprehensive morphological matrix with 120 characters was used as a basis to map morphological characters (Lohmann, 2003; Lohmann et al., in prep.) onto the molecular phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006). This analysis identified morphological synapomorphies that characterize particular clades, most of which are vegetative rather than reproductive. In addition, several characters were shown to represent useful traits for the identification of particular genera, although they are not strictly synapomorphic. A detailed list of characters that aid in identification of the Bignonieae genera is presented in Tables 3 and 4, and below we present an overview of Bignonieae morphology. See Gentry (1980), Lohmann (2004), and Fischer et al. (2004) for broader descriptions of morphological traits associated with all Neotropical Bignoniaceae; the terminology and interpretation of morphological traits here follow those works.

Dimorphic juvenile growth form. Two genera of Bignonieae, *Amphilophium* and *Dolichandra*, are characterized by small-leaved juvenile forms that differ markedly from the spreading or pendulous reproductive form (Fig. 6C). The juvenile forms grow closely appressed to the bark of the supporting tree, but in each genus the attachment to the tree trunk is different. In *Amphilophium* the stems attach to the bark of the supporting tree by disk-tipped tendrils, while in *Dolichandra* they attach by cat's-claw tendrils. Dimorphic juvenile growth is also found in one species of *Mansoa*, which has disk-tipped tendrils.

Phloem wedges in the stem. The wood anatomy of the tribe Bignonieae is notable for its anomalous secondary growth (Solereder, 1908). This is formed by segments of the cambium that fail to produce secondary xylem while continuing production of phloem (Dobbins, 1971; Pace, 2009, 2011), resulting in a secondary xylem that is interrupted by deep wedges of phloem. All Bignonieae lianas have this uncommon wood structure, which is unknown elsewhere in the family and a synapomorphy of the tribe; however, this is lacking in some Bignonieae species that grow as shrubs. Stems of *Perianthomega* have four phloem arcs (Fig. 17D), while several genera have four phloem wedges (e.g., *Adenocalymma*, *Fridericia*, *Tanaecium*), others consistently have phloem wedges produced in multiples of four (e.g., *Amphilophium*, *Anemopaegma*, *Bignonia*), and *Dolichandra* has multiple dissected phloem wedges that are a synapomorphy of this last genus.

Consistency of the pith. While most members of the tribe Bignonieae have a solid stem pith, a hollow pith is present in *Stizophyllum* and is a synapomorphy of this genus. Gentry (1980) noted that some species of *Pleonotoma* also have stems that may tardily become hollowed with age, but these stems are solid initially.

Branchlet and petiole cross-section shape. In members of the tribe Bignonieae the branchlets may be cylindrical, tetragonal, or hexagonal in cross-section. The shape helps to identify particular clades. However, various branchlet shapes have arisen multiple times in the tribe and are not synapomorphies of any particular clade, except tetragonal stems with the angles winged are a synapomorphy of *Pleonotoma*. Petioles, on the other hand, are generally cylindrical in cross-section throughout the tribe except for those of *Pleonotoma*, which are tetragonal and represent another synapomorphy of this genus.

Petiole and petiolule bases. In most members of the tribe Bignonieae the petioles and petiolules are straight at the base and not articulated. *Adenocalymma* alone has pulvinate and articulated connections between the petioles and petiolules, which represents a synapomorphy for this genus (Fig. 5A, D).

Interpetiolar gland fields. The interpetiolar gland fields are groups of glands borne on the stems between the petioles, which are often present at the nodes in members of the tribe Bignonieae. Their presence has frequently been used to characterize genera. Such glands are found in various genera (e.g., *Fridericia*, *Pachyptera*, *Tanaecium*), and although they have arisen multiple times in Bignonieae (Nogueira et al., 2012b), these traits are often useful for generic identification.

Interpetiolar ridges. The interpetiolar ridges are two transverse ridges on the stem running between the petioles. This character is found in several genera of the tribe, but may vary within a genus. Usually these are developed as two separate or discontinuous ridges, with one on each interpetiolar side of the stem. However, in *Martinella* the interpetiolar ridges are fused to form a continuous ring that completely surrounds the stem, representing a synapomorphy of this genus. Interpetiolar ridges are generally lacking

Table 2. Bignonieae genera recognized under the most significant classification systems.

Don (1838)	de Candolle (1838)	Endlicher (1839)	Meisner (1840, 1843)	de Candolle (1845)	Bureau (1864)	Bentham (1876)	Baillon (1888)	Schumann (1894)	Gentry (1973a to 1993)	Lohmann & Taylor, this publication
Amphilophium	*Amphilophium*	*Amphilophium*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma* *Anisostichus*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma*	*Adenocalymma* *Amphilophium* *Anemopaegma*
	Arrabidaea		*Arrabidaea*	*Arrabidaea*	*Arrabidaea*	*Arrabidaea*	*Arrabidaea*	*Arrabidaea*	*Arrabidaea*	
Bignonia	*Bignonia*	*Bignonia*	*Bignonia*	*Bignonia*	*Bignonia* *Callichlamys*	*Bignonia* *Callichlamys*	*Bignonia* *Callichlamys*	*Bignonia* *Callichlamys*	*Bignonia* *Callichlamys* *Ceratophytum*	*Bignonia* *Callichlamys*
							Clytostoma *Cremastus*	*Clytostoma* *Cremastus*	*Clytostoma*	
	Cuspidaria		*Cuspidaria*	*Cuspidaria*	*Cuspidaria*	*Cuspidaria*	*Cuspidaria* *Cydista*	*Cuspidaria* *Cydista*	*Cuspidaria* *Cydista* *Distictella*	*Cuspidaria*
			Distictis	*Distictis*	*Distictis* *Dolichandra*	*Distictis*	*Distictis* *Dolichandra* *Doxantha*	*Distictis* *Dolichandra* *Doxantha*	*Distictis* *Dolichandra*	*Dolichandra*
Fridericia	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*	*Fridericia*
						Glaziova	*Glaziova*	*Glaziova*	*Gardnerodoxa* *Glaziova*	
	Haplolophium	*Haplolophium*	*Haplolophium*	*Haplolophium*	*Haplolophium*	*Haplolophium*	*Haplolophium*	*Haplolophium*	*Haplolophium*	
							Levya	*Levya*	*Leucocalantha*	
	Lundia		*Lundia*	*Lundia* *Macfadyena*	*Lundia* *Macfadyena*	*Lundia* *Macfadyena*	*Lundia* *Macfadyena*	*Lundia* *Macfadyena*	*Lundia* *Macfadyena*	*Lundia*
					Macrodiscus		*Macrodiscus*	*Macranthisiphon* *Macrodiscus*	*Macranthisiphon*	
									Manaosella	*Manaosella*
	Mansoa		*Mansoa*	*Mansoa*	*Mansoa*		*Mansoa* *Martinella*	*Mansoa* *Martinella*	*Mansoa* *Martinella*	*Mansoa* *Martinella*
						Melloa	*Melloa*	*Melloa*	*Melloa*	
							Memora	*Memora*	*Memora*	
							Mussatia	*Mussatia*	*Mussatia*	
							Neojobertia	*Neojobertia*	*Neojobertia*	*Neojobertia*
							Neomacfadyena	*Neomacfadyena*		
			Pachyptera	*Pachyptera*	*Pachyptera*					*Pachyptera*
								Parabignonia	*Parabignonia*	

Table 2. Continued.

Don (1838)	de Candolle (1838)	Endlicher (1839)	Meisner (1840, 1843)	de Candolle (1845)	Bureau (1864)	Bentham (1876)	Baillon (1888)	Schumann (1894)	Gentry (1973a to 1993)	Lohmann & Taylor, this publication
							Paragonia	*Paragonia*	*Paragonia*	
							Paramansoa	*Paramansoa*		
							Perianthomega	*Perianthomega*		*Perianthomega*
									Periarrabidaea	
							Petastoma			
							Phadranthus	*Phaedranthus*		
							Phryganocydia	*Phryganocydia*	*Phryganocydia*	
									Piriadacus	
			Pithecoctenium	*Pithecoctenium*	*Pithecoctenium*	*Pithecoctenium*	*Pithecoctenium*	*Pithecoctenium*	*Pithecoctenium*	
							Pleonotoma	*Pleonotoma*	*Pleonotoma*	*Pleonotoma*
									Potamoganos	
									Pseudocatalpa	
			Pyrostegia				*Pyrostegia*	*Pyrostegia*	*Pyrostegia*	*Pyrostegia*
									Roentgenia	
					Saldanhaea		*Saldanhaea*	*Saldanhaea*		
							Sanhilaria	*Sanhilaria*		
									Saritaea	
			Schizopsis							
							Setilobus	*Setilobus*		
									Spathicalyx	
							Stizophyllum	*Stizophyllum*	*Stizophyllum*	*Stizophyllum*
			Tanaecium	*Tanaecium*			*Tanaecium*	*Tanaecium*	*Tanaecium*	*Tanaecium*
					Tynanthus		*Tynanthus*	*Tynanthus*	*Tynanthus*	*Tynanthus*
									Xylophragma	*Xylophragma*

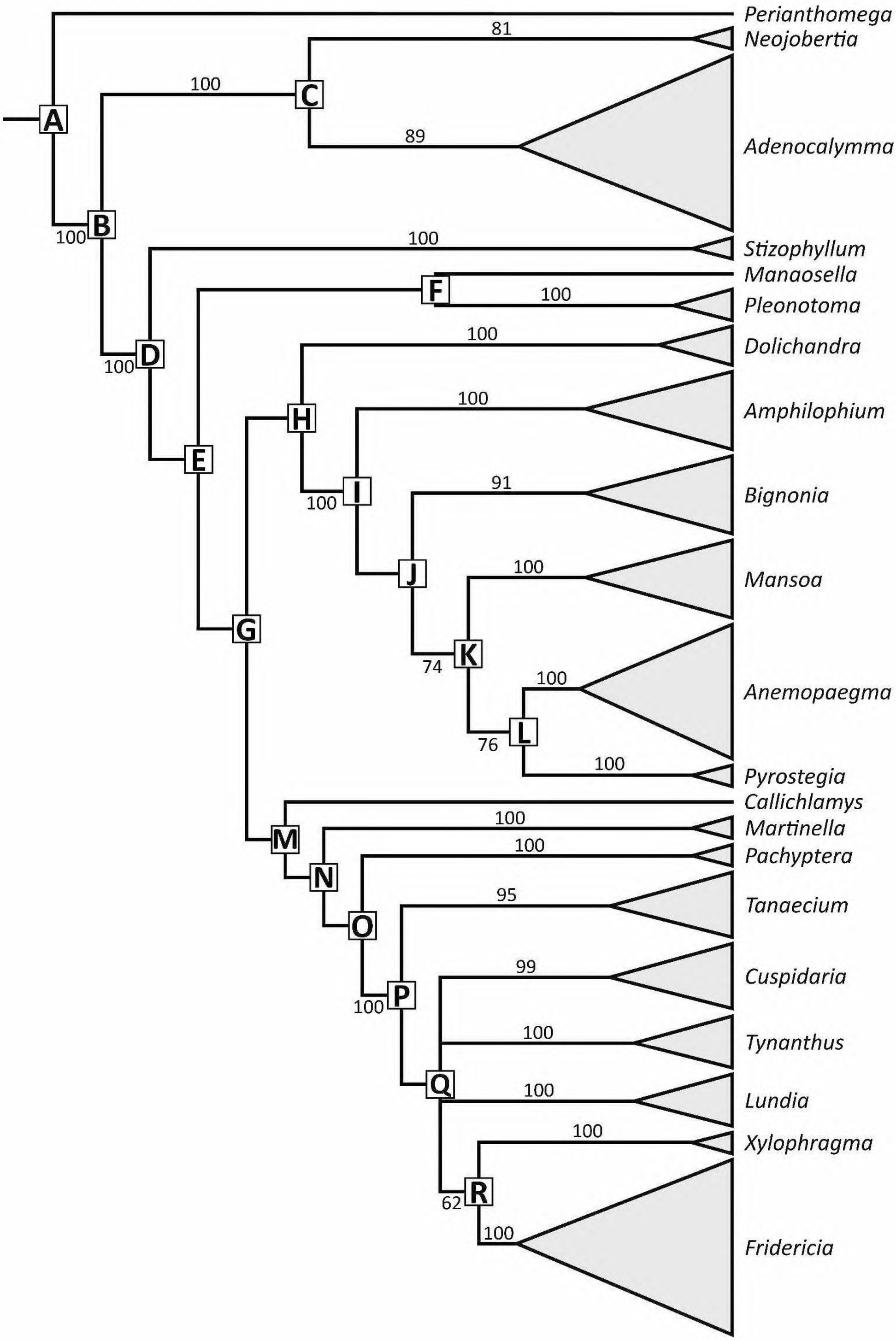


Figure 2. Schematic diagram summarizing phylogenetic relationships among the genera of Bignonieae, with nodes labeled by letters and the genera recognized labeled as terminal taxa. Relationships within the Core Bignonieae clade are those hypothesized by the molecular analyses of Lohmann (2006); support values are from the combined molecular results, except for values for the Bignonieae (node A), Core Bignonieae clade (node B), and *Neojobertia–Adenocalymma* clade (node C), which are taken from analyses of *ndhF* alone.

Table 3. Vegetative characters useful in recognizing genera; characters within parentheses are less common.

	Dimorphic juvenile growth	Phloem wedges in stem	Branchlet section	Interpetiolar gland field	Prophylls of axillary buds	Leaf type	Tendril type
Adenocalymma	absent	four	cylindrical	absent (present)	subulate, or foliaceous	2- or 3-foliolate, biternate, or biternate-pinnate	simple (trifid)
Amphilophium	present (absent)	multiples of four	hexagonal, or cylindrical	absent	foliaceous	2- or 3-foliolate	trifid (multifid) with disks
Anemopaegma	absent	multiples of four	cylindrical	absent (present)	foliaceous, or minute	2- or 3(5)-foliolate	trifid (simple)
Bignonia	absent	multiples of four	cylindrical, and/or tetragonal	absent	bromeliad, foliaceous (minute)	2- or 3-foliolate	simple (minutely trifid, or multifid)
Callichlamys	absent	four	cylindrical	absent	minute	2- or 3-foliolate	simple
Cuspidaria	absent	four	cylindrical (tetragonal)	present	minute	2- or 3-foliolate (biternate)	simple
Dolichandra	present	multiple dissected	cylindrical	present (absent)	subulate	2- or 3-foliolate	trifid and cat's claw
Fridericia	absent	four	cylindrical	present (absent)	minute	1-, 2-, or 3-foliolate	simple
Lundia	absent	four	cylindrical	present	minute	2- or 3-foliolate	simple, or trifid
Manaosella	absent	four	cylindrical	absent	minute	2- or 3-foliolate	multifid with disks
Mansoa	absent (present)	multiples of four	cylindrical, becoming angular	absent (present)	minute, or bromeliad	2- or 3-foliolate	trifid
Martinella	absent	four	cylindrical, or tetragonal	absent	minute	2- or 3-foliolate	trifid
Neojobertia	absent	four	hexagonal	absent	subulate	biternate, or biternate-pinnate	trifid, multifid
Pachyptera	absent	four	cylindrical, or tetragonal	present	minute, or ensiform	2- or 3-foliolate	trifid
Perianthomega	absent	four	cylindrical	absent	minute	biternate	simple
Pleonotoma	absent	four	tetragonal	absent	foliaceous	biternate, or biternate-pinnate	trifid
Pyrostegia	absent	multiples of four	hexagonal	absent	minute	2- or 3-foliolate	trifid
Stizophyllum	absent	four	cylindrical	absent	foliaceous	2- or 3-foliolate	trifid
Tanaecium	absent	four	cylindrical (tetragonal)	absent, or present	bromeliad, or subulate	2- or 3-foliolate	simple (bifid), or trifid
Tynanthus	absent	four	cylindrical	absent	minute, or foliaceous	2- or 3-foliolate	trifid
Xylophragma	absent	four	cylindrical	present	minute, or bromeliad	2- or 3(5)-foliolate	simple

Table 4. Reproductive characters useful in recognizing genera; characters within parentheses are less common.

	Inflorescence type	Calyx shape	Corolla color	Corolla indument	Ovules series per placenta	Fruit shape	Fruit ornamentation
Adenocalymma	raceme (thyrse)	cupular	yellow (white or red)	puberulous (villose)	one	linear or elliptic	smooth
Amphilophium	raceme or thyrse	cupular	yellow or white (magenta, pink, or red)	puberulous, villose	many	elliptic	tuberculate or echinate
Anemopaegma	raceme, cyme, compound thyrse, or fascicle	cupular	yellow (white or red)	puberulous (villose)	many	orbicular	smooth
Bignonia	cyme, thyrse, raceme, or fascicle	cupular or tubular	magenta, pink (yellow, white, or red)	glabrous, puberulous, or villose	one	linear or elliptic	smooth, echinate, or tuberculate
Callichlamys	raceme	spathaceous	yellow	puberulous	many	elliptic	smooth
Cuspidaria	compound thyrse	cupular	magenta or pink (red)	glabrous or villose	two	linear	smooth, with two ridges, or winged
Dolichandra	cyme or thyrse	cupular or spathaceous	yellow or red	glabrous	many (one)	linear (elliptic)	smooth, tuberculate, or winged
Fridericia	compound thyrse (thyrse)	cupular or tubular (urceolate)	magenta or pink (white or red)	villose (glabrous)	one	linear	smooth
Lundia	compound thyrse	cupular (tubular)	white (red)	villose	two	linear	smooth or ridged (winged)
Manaosella	raceme	spathaceous	yellow (magenta or pink)	glabrous	two	linear	smooth
Mansoa	thyrse (fascicle)	cupular	magenta or pink	puberulous	two	linear	smooth or ridged (tuberculate)
Martinella	thyrse	tubular	magenta, or pink, or red	glabrous	one	linear	smooth
Neojobertia	raceme at base, thyrse at apex	tubular or spathaceous	yellow or red	glabrous	one	linear	smooth
Pachyptera	raceme	tubular	white	villose	one	linear	smooth
Perianthomega	raceme	tubular	white	glabrous	one	linear	smooth
Pleonotoma	raceme	cupular, tubular	white or yellow	glabrous, puberulous	two	linear	smooth
Pyrostegia	corymb	cupular	orange or white	puberulous	two	linear	smooth
Stizophyllum	raceme	urceolate	magenta or white	pubescent	two	linear	smooth
Tanaecium	thyrse or cyme	cupular	yellow, magenta, or white	villose	one (two)	linear (elliptic)	smooth
Tynanthus	compound thyrse	cupular	white	villose	two	linear	smooth or winged
Xylophragma	compound thyrse (thyrse)	cupular	magenta or pink	villose	many	linear	smooth

in taxa with interpetiolar glands, although this is not a strict correlation.

Prophylls of the axillary buds. Even though members of the family Bignoniaceae lack stipules, the scales of the axillary buds are often enlarged and modified into stipule-like structures, which have sometimes been referred to as pseudostipules (e.g., Gentry, 1980) or cataphylls; these structures are here called prophylls. Prophylls may be minute and triangular (Fig. 11K), leaflike (i.e., foliaceous and green; Figs. 5C, 11A, 11F, 11J, 11O, 11S), subulate (Fig. 11E), bromeliad-like (Fig. 18B), or ensiform and usually rigid (Fig. 17B). The term bromeliad-like (e.g., Gentry, 1980) refers to an axillary bud with several prophylls that are generally subulate-lanceolate in shape and tightly grouped or whorled, and resemble a small plant of the Bromeliaceae; these are found in several genera. Most of these prophyll forms have arisen multiple times in the tribe, but the combination of bromeliad-like and leaflike prophylls in the same individual is unique to species of *Bignonia*, and ensiform prophylls arranged in multiple series are unique to *Pachyptera*. Our knowledge of this character is currently limited, and detailed morphological and developmental study is needed.

Vegetative odor. A strong smell of clove in the foliage is unique to and a synapomorphy of *Tynanthus*, while a strong smell of garlic is a synapomorphy of *Mansoa*. These strong odors are thought to be associated with chemical defense against herbivores.

Leaf form. The leaves of most members of the tribe Bignonieae are (1)2- or 3(or 5)-foliolate with the terminal leaflet modified into a tendril (e.g., Figs. 9C, 10A, 14E). Biternately compound (Fig. 5D) or biternately pinnate (Fig. 5A) leaves with the terminal blade usually modified into a tendril are present in several early-diverging lineages of Bignonieae. Among these lineages, only *Perianthomega* has exclusively biternately compound leaves that lack tendrils, and it also has petioles that are twining and modified as tendrils (Fig. 17C).

Leaflets. The leaflets in members of the tribe Bignonieae are generally well developed, and very generally elliptic to ovate. The venation is pinnate, and most often eucamptodromous to festooned-broquidodromous (e.g., Figs. 7A, 7D, 7G, 7J, 7O). In some species, the basalmost pair of secondary axes is very well developed and the venation approaches triplinerved. The lamina is pellucid-punctate in

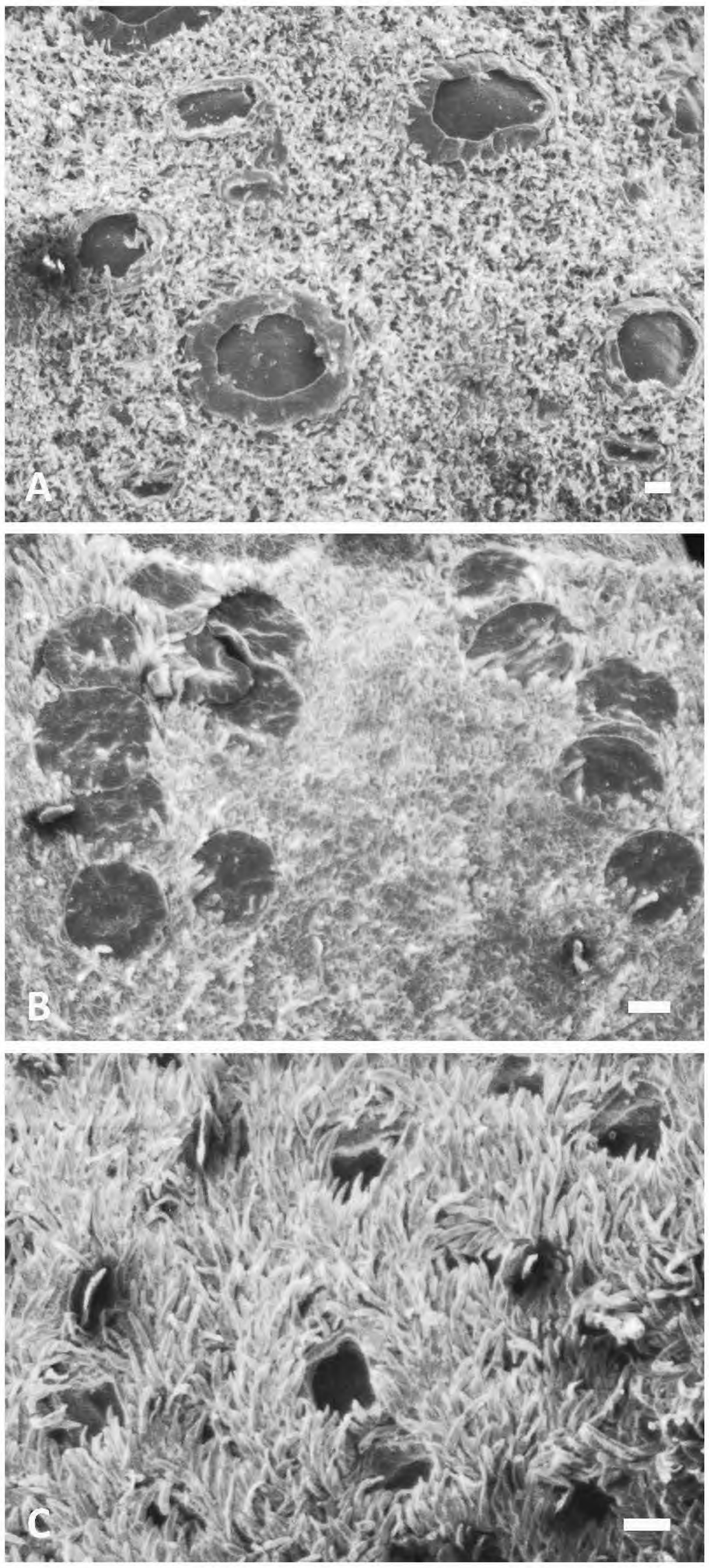


Figure 3. Calyx glands in Bignonieae. —A. Volcano-shaped glands of *Adenocalymma* Mart. ex Meisn., exemplified by *A. trichocladum* (DC.) L. G. Lohmann. —B. Plate-shaped glands of most Bignonieae, as represented by *Fridericia spicata* (Bureau & K. Schum) L. G. Lohmann. —C. Glands immersed in the epidermis of *Amphilophium* Kunth, as shown by *A. mansoanum* (DC.) L. G. Lohmann. Magnification bars = 100 μm. A illustrated from *Daly et al. 560* (MO); B from *Pires et al. 795* (MO); C from *Hatschbach et al. 28074* (MO).

Stizophyllum, as well as in some species of *Pyrostegia* and *Amphilophium*, and often has patelliform (i.e., saucer-shaped or plate-shaped), peltate, and/or stipitate trichomes distributed sparsely across it and/or in the vein axils on both surfaces (Nogueira et al., 2013).

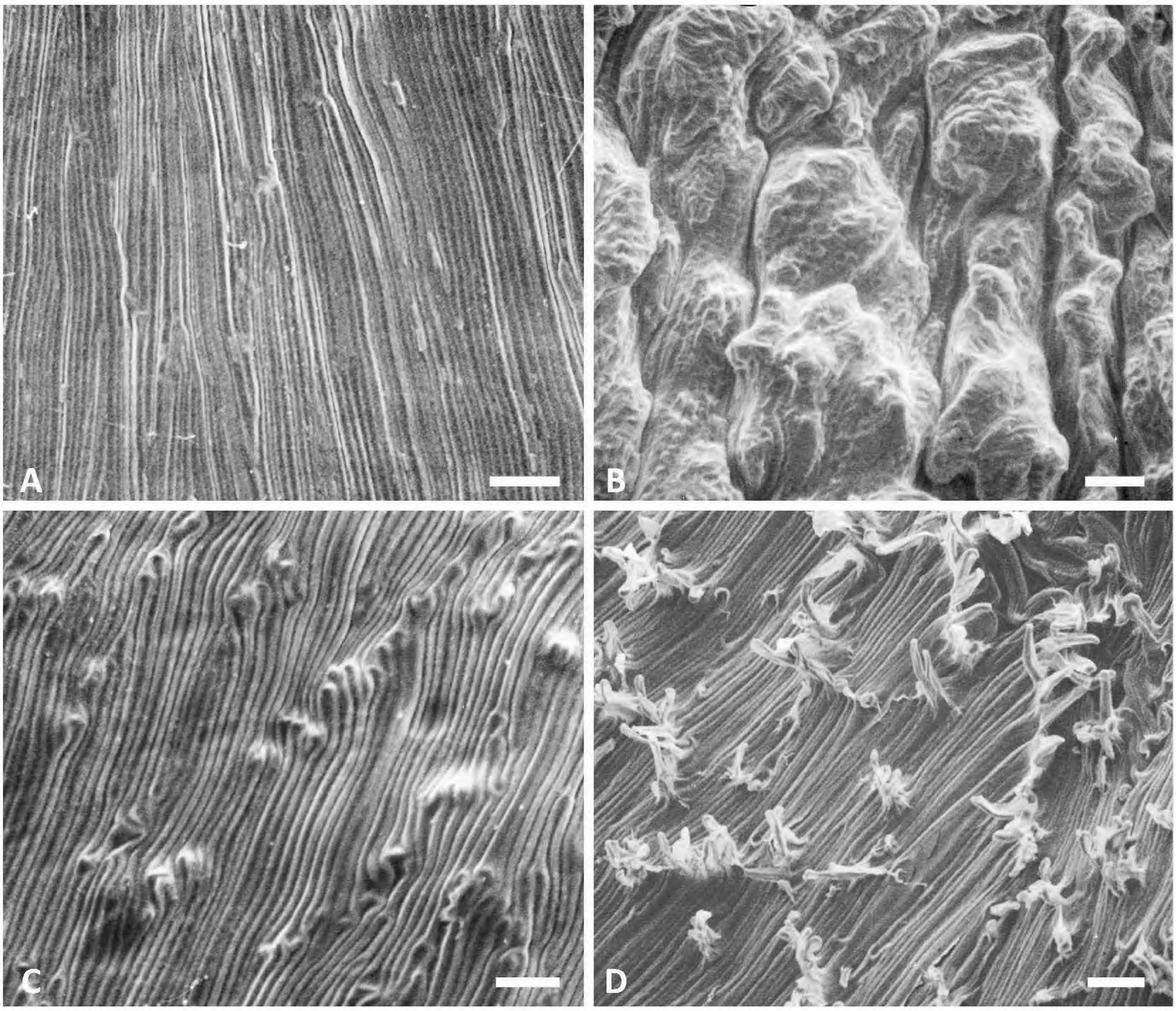


Figure 4. Seed coat in Bignonieae. —A. Smooth seed coat found in most Bignonieae, as shown by *Fridericia rego* (Vell.) L. G. Lohmann. —B. Rough seed coat of *Neojobertia* Baill., exemplified by *N. candolleana* (Mart. ex DC.) Bureau & K. Schum. C, D. Papillate seed coat found in *Amphilophium* Kunth. —C. *Amphilophium granulosum* (Bureau & K. Schum.) L. G. Lohmann. —D. *Amphilophium lohmanniae* (A. Pool) L. G. Lohmann. Magnification bars = 100 μm. A illustrated from *Folle 3989* (MO); B from *Alencar 577* (MO); C from *Prance 22656A* (MO); D from *Lohmann & da Silva 20* (MO).

Tendril type. The tendrils vary from simple, trifid, or bifid to multifid (i.e., each segment is parted into three multiple times), and the different forms have arisen repeatedly in the tribe Bignonieae (Lohmann, 2003; Sousa-Baena et al., 2013, 2014; Lohmann et al., in prep.). *Amphilophium* and one species of *Mansoa* have trifid tendrils with the tips modified into adhesive disks, while *Manaosella* alone has multifid tendrils with the tips modified into adhesive disks. The tendrils of *Dolichandra* are also unique, with thickened and bent segments or arms forming a clawlike or uncinate structure.

Inflorescence type. Taxonomic use of inflorescence type has been rather neglected in Bignoniaceae. Any branching inflorescence has generally been referred to as paniculate in a broad sense by earlier workers (e.g., Gentry, 1973a, 1973b, 1976, 1979). However, several different inflorescence types can be distinguished within this tribe, including cymes, racemes, corymbs, thyrses, compound thyrses, and fascicles. While most inflorescence types have arisen multiple times in Bignonieae (Lohmann, 2003; Lohmann et al., in prep.) and thus are not unique to any particular genus, corymbose inflorescences are a synapomorphy of *Pyrostegia*.

Calyx form. The calyx is usually a large and significant structure in the tribe Bignonieae, and its form varies widely in this tribe. This character has been one of the most widely used to distinguish genera of this tribe (e.g., Gentry 1973a, 1973b, 1976, 1979), although there is wide variation in calyx form within many genera. Gentry himself (1980) noted that

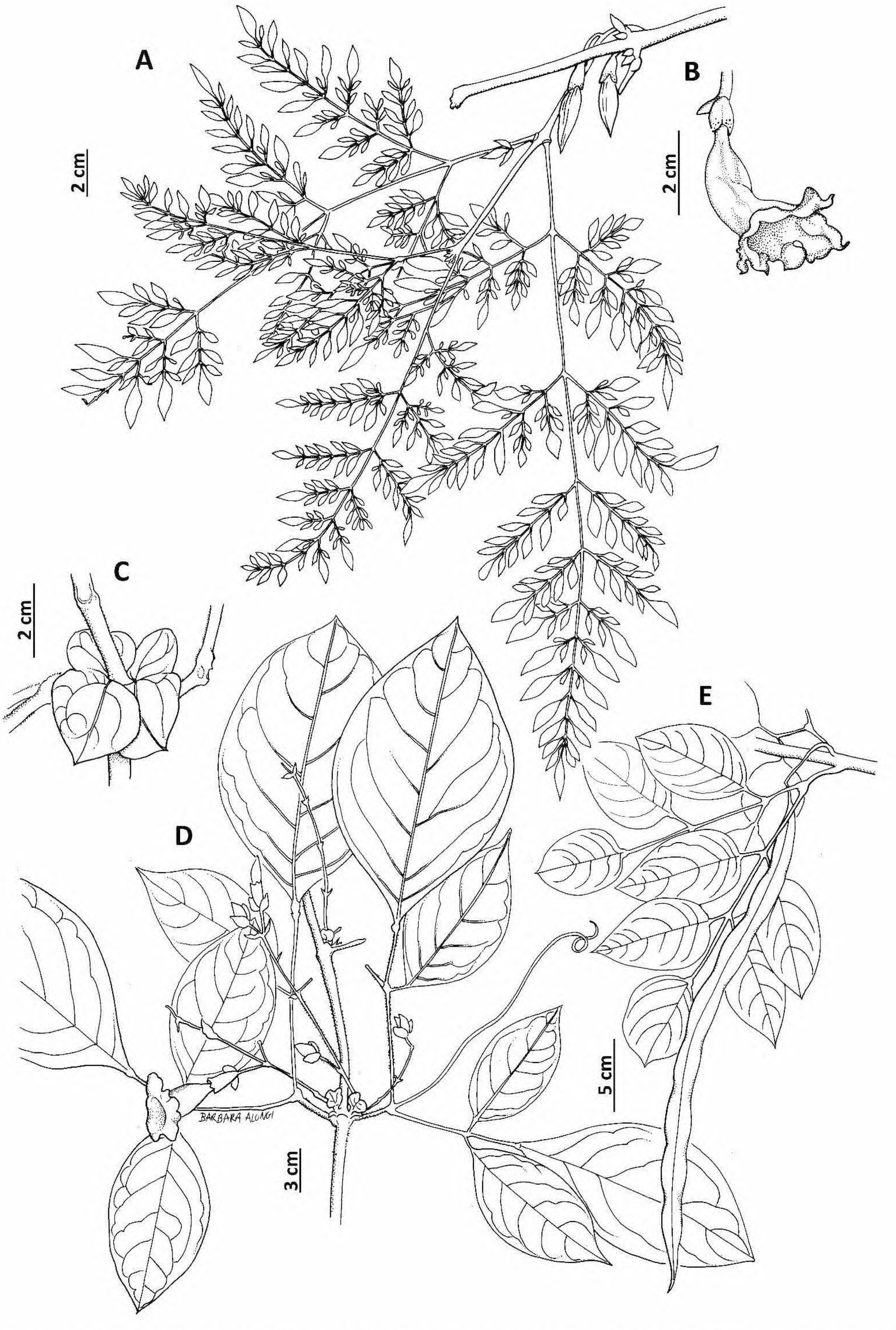


Figure 5. Representative morphological traits of *Adenocalymma* Mart. ex Meisn. A, B. *Adenocalymma moringifolium* (DC.) L. G. Lohmann. —A. Flowering branch showing biternately pinnate leaves. —B. Flower. C–E. *Adenocalymma adenophorum* (Sandwith) L. G. Lohmann. —C. Foliaceous prophylls. —D. Flowering branch showing biternately compound leaves. —E. Fruit. A, B illustrated from *Lohmann et al. 13* (MO); C, D from *Lohmann et al. 14* (MO); E from *Lohmann et al. 30* (MO).

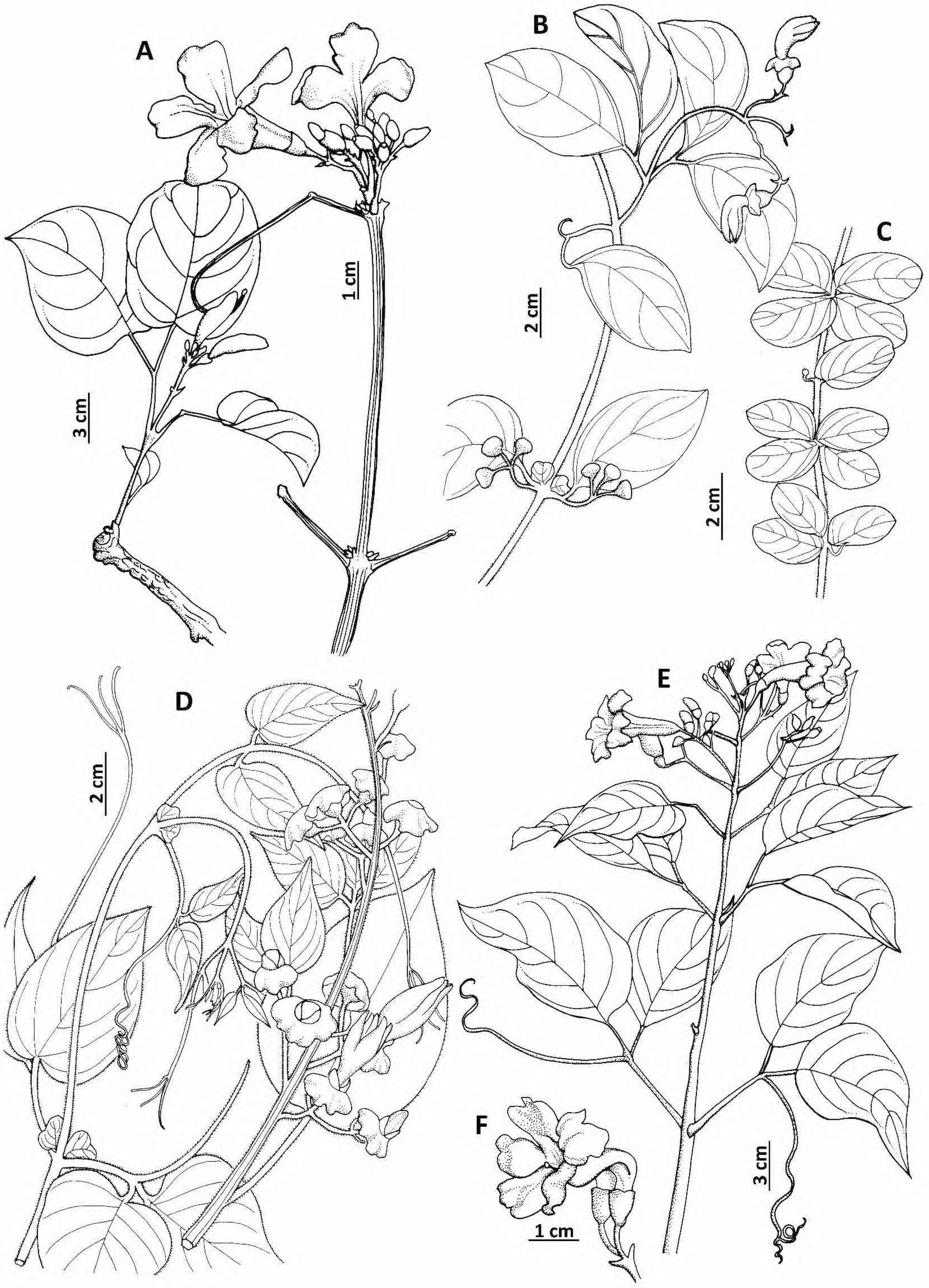


Figure 6. Representative morphological traits of *Amphilophium* Kunth. —A. *Amphilophium pulverulentum* (Sandwith) L. G. Lohmann (this species was previously included in *Distictis* Mart. ex Meisn.), flowering branch. B, C. *Amphilophium bauhinioides* (Bureau ex Baill.) L. G. Lohmann (previously in *Glaziova* Bureau). —B. Flowering branch. —C. Dimorphic juvenile form. —D. *Amphilophium aschersonii* Ule, flowering branch. —E, F. *Amphilophium elongatum* (Vahl) L. G. Lohmann (previously in *Distictella* Kuntze). —E. Flowering branch. —F. Flower. A illustrated from *Hopkins 1551* (MO); B from *Kuhlmann 6510* (MO); C from *Lutz 2066* (MO); D from *Vigo 7276* (MO); E, F from *Lohmann et al. 70* (MO).

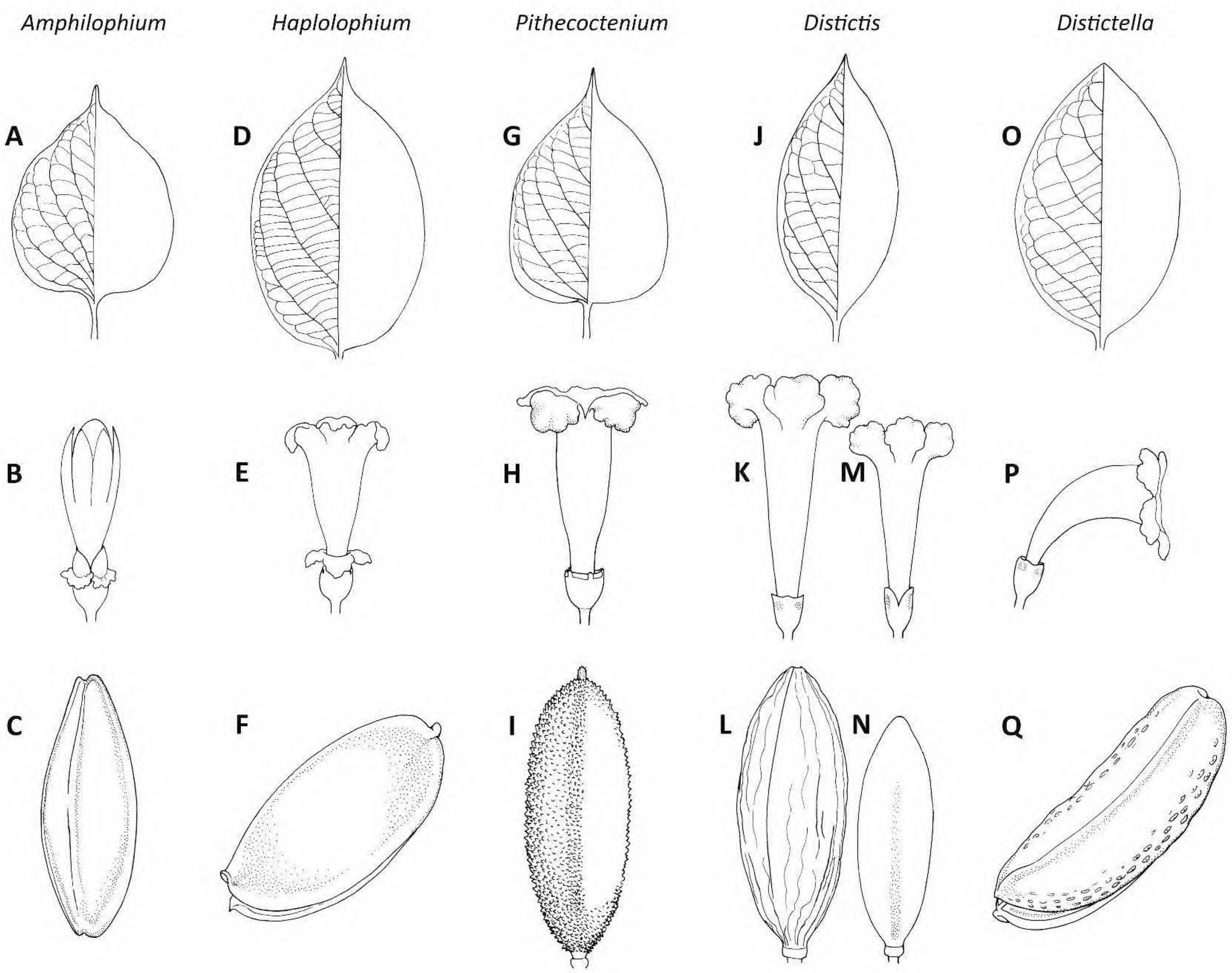


Figure 7. Comparison of leaves (top row), flowers, and fruits (in lower rows, respectively) among different species of *Amphilophium* Kunth; names above columns indicate the genera in which these species were previously included. A–C. *Amphilophium paniculatum* (L.) Kunth. D–F. *Amphilophium rodriguesii* (A. H. Gentry) L. G. Lohmann. G–I. *Amphilophium crucigerum* (L.) L. G. Lohmann. J–L. *Amphilophium buccinatorium* (DC.) L. G. Lohmann. M, N. *Amphilophium pulverulentum* (Sandwith) L. G. Lohmann. O–Q. *Amphilophium magnoliifolium* (Kunth) L. G. Lohmann. A, B illustrated from *Zardini & Velazquez 18163* (MO); C from *Croat s.n.* (MO); D, E from *Solomon 6295* (MO); F from *Cremers et al. 12485* (MO); G–I from *Zardini 6224* (MO); J–L from *Boutin 1900* (MO); M, N from *Gentry et al. 21308* (MO); O, P from *Allen et al. 3210* (MO); Q from *Boutin 3317* (MO).

this infrageneric variation has been underappreciated, and also that calyx form varies markedly within some individual species. The general calyx shape ranges from cupular to tubular or urceolate, with the form of its opening varied. The calyx is usually truncate to usually 5-lobed, with the lobes triangular and short to well developed or occasionally filiform. The calyx may also be regularly to irregularly bilabiate, to 3- or 4-lobed, occasionally spathaceous (i.e., fused completely in bud and opening by a lateral slit) in a few genera such as *Callichlamys* (Fig. 13A), *Manaosella* (Fig. 16F), and some species of *Neojobertia* (Fig. 16C), or calyptrate (i.e., fused and with the top portion dehiscing transversally or in a circumscissile fashion) in *Lundia* (Kaehler et al., 2012). The double-calyx form found in *Amphilophium* is notable (Figs. 6D, 7B, E), with the calyx divided circumferentially in its middle or upper part into two concentric layers, one that encloses the corolla (the "Manschette" or cuff, Schumann, 1894: 203–204; the "thick inner margin," Gentry, 1980: 17) and another layer external to it that often spreads and is crisped, similarly to a skirt (the "Anhang" or appendage, Schumann, 1894: 203–204; the "submarginal rim," Gentry, 1980: 17). Several appendages are also produced on the outside of the calyx limb in at least one species of *Bignonia*. The texture of the calyx also varies markedly, generally from membranaceous to coriaceous except in *Callichlamys*, where this is spongy (Fig. 13A).

Calyx glands. Glands in the calyx of members of the tribe Bignonieae exude a sugary nectar that attracts ants, which presumably play an important role in the protection of the flower from nectar robbers that would otherwise puncture the corolla at the base of the tube

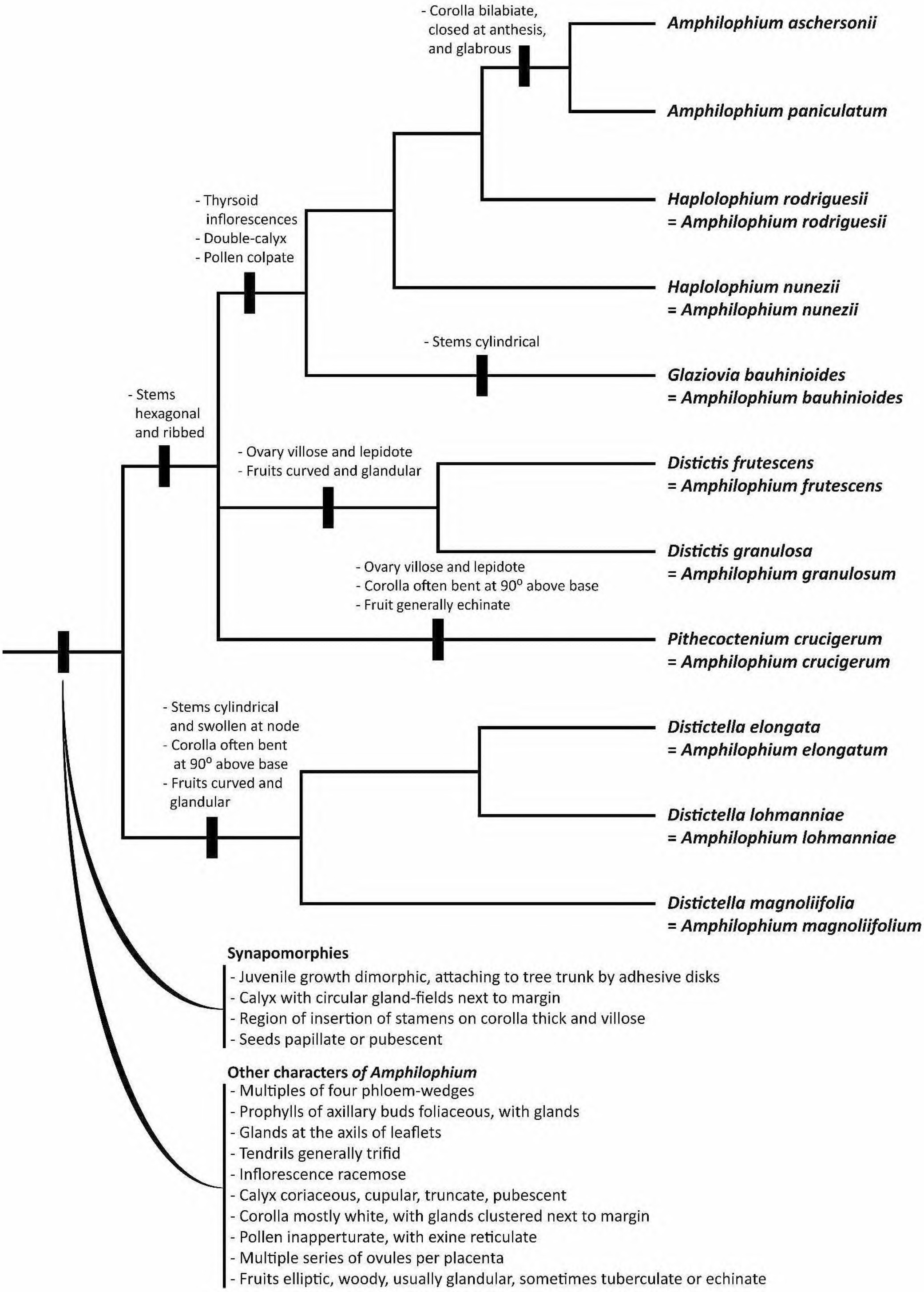


Figure 8. Phylogenetic hypothesis of *Amphilophium* Kunth, with morphological characters mapped on the diagram. Names of the terminal taxa indicate the genera in which these species were previously included and changes in the classification proposed here are indicated. The synapomorphies represent unique characters that diagnose the genus; the other characters are found in *Amphilophium* and additionally describe the genus. Relationships depicted follow Lohmann (2006).

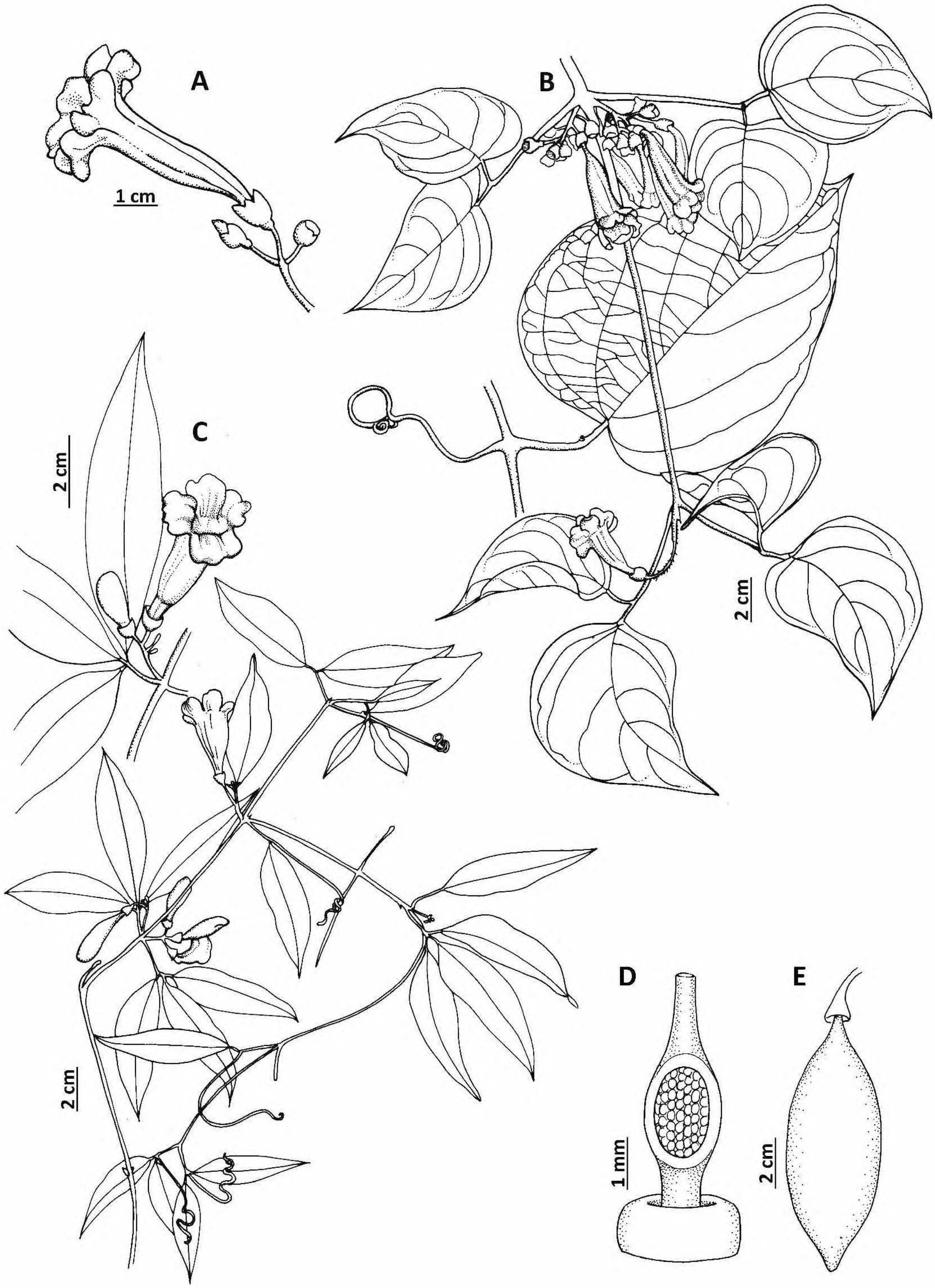


Figure 9. Representative morphological traits of *Anemopaegma* Mart. ex Meisn. A, B. *Anemopaegma oligoneuron* (Sprague & Sandwith) A. H. Gentry. —A. Flower. —B. Flowering branch. C–E. *Anemopaegma foetidum* Bureau & K. Schum. —C. Flowering branch. —D. Stipitate ovary. —E. Stipitate and orbiculate fruit. A, B illustrated from *Lohmann et al. 76* (MO); C, D from *de Souza et al. 252* (MO); E from *Sothers et al. 1017* (MO).

to steal nectar (Gentry, 1974a). These glands are generally patelliform (Fig. 3B), and are variously scattered over the calyx, grouped near the margins, or occasionally solitary along the margins (some species of *Fridericia*) or arranged in lines (*Pachyptera*, *Pleonotoma*). In two genera the glands are unusual in being deeply immersed in the epidermis. Investigation of the ultrastructure of these unusual glands found those of *Amphilophium* (Fig. 3C) to be otherwise similar to the surface glands, but the immersed glands of *Adenocalymma* to be different. These last are urceolate or tubular in form with extended margins that protrude above the leaf surface (Fig. 3A), a form apparently restricted to this genus and here called volcano-shaped glands.

Corolla. Corolla shape and color have been the predominant characters used to diagnose genera in previous classification systems (e.g., de Candolle, 1845; Bureau, 1864; Baillon, 1888; Gentry, 1973a). Gentry (1974a) in particular catalogued several distinctive corolla forms that he used to distinguish several genera. However, phylogenetic reconstructions of selected flower traits show that particular corolla colors and most of the corolla forms have arisen multiple times within this tribe (Lohmann, 2003; Alcantara & Lohmann, 2010, 2011), and this together with the similar variation in fruit morphology explain in large part why previous classifications of the tribe Bignonieae have been unstable and phylogenetically unsatisfactory. In general the corollas in the tribe Bignonieae are rather large (2–6 cm long), white to brightly colored and often also marked with nectar guides, weakly to markedly zygomorphic, and 5-lobed. The corollas vary widely among the species in a number of features including color and color pattern, size, and orientation of the lobes. Only three genera of Bignonieae, *Amphilophium*, *Tynanthus*, and *Bignonia*, have unique corolla morphologies (the Amphilophium-type, the Tynanthus-type, and the Mimetic-type, respectively; Gentry, 1974a; Alcantara & Lohmann, 2010), which are synapomorphies of these genera. The corolla tube and lobes of *Amphilophium* are unique in their thick texture of the outer surface and internally at the region of the stamen insertion, which presumably is an adaptation for carpenter-bee pollination (Gentry, 1974a; Fig. 6F). The corollas of *Tynanthus* are relatively small (up to ca. 1 cm long), and bilabiate with the two upper lobes fused (Fig. 18E); they are thought to be adapted for butterfly pollination (Gentry, 1974a). The corollas of *Bignonia* are flattened abaxially and have nectar guides, even though they lack nectar disks; these flowers are thought to be adapted for pollination by deceit, in which pollination is dependent on exploratory visits by nectar-seeking bees (Gentry, 1974a; Umaña et al., 2011).

Corolla glands. Most genera of the tribe Bignonieae lack glands on the corolla, but these are present in a few genera. The corolla glands are arranged in lines in the upper (i.e., distal) part of the corolla tube in *Adenocalymma*, *Anemopaegma*, and *Pachyptera*, and in lines near the corolla margins in *Amphilophium*.

Corolla aestivation. All members of the tribe Bignonieae have imbricate corolla aestivation. *Pyrostegia* was once thought to have valvate aestivation (e.g., de Candolle, 1845; Miers, 1863; Schumman, 1894; Bureau & Schumman, 1896; Gentry, 1973b), but detailed analysis of this character (Pool, 2008) found that although the lobes are valvate at their bases, their apices are imbricate. This unusual arrangement is a synapomorphy of this genus.

Stipitate ovary. The ovaries of members of the tribe Bignonieae are sessile except for those of *Anemopaegma*, which are distinctly stipitate (Fig. 9D). This structure persists on the fruits, which are also stipitate, and is a synapomorphy of the genus (Fig. 9E).

Stamens. As noted by Gentry (1980), the androecium varies markedly within the family Bignoniaceae, but much less within the tribe Bignonieae. In general members of the tribe Bignonieae have four didynamous stamens with well-developed filaments and one posterior staminode, except for one species of *Tanaecium* that has two stamens and no staminodes. In most members of the tribe, the anthers are glabrous; *Lundia* is separated in part by its villous anthers, but pubescent anthers are also found in a few species of some other genera (e.g., *Pachyptera*). The anthers are bithecal, and the arrangement of the thecae varies. In most of the tribe the thecae are parallel, but sometimes they are attached at the apex and separated below that attachment with the bases spreading or divergent. Several genera have unusual anthers with forward-curved thecae: in these the thecae are attached at their apices, and have their bodies curved in a U shape so their bases are ascending and often positioned above their apices (*Cuspidaria*, *Tynanthus*, some species of *Fridericia*).

Fruit characters. All members of the tribe Bignonieae have septicidal capsules, and this is a synapomorphy of this tribe (Gentry, 1980; Olmstead et al., 2009). Fruit dehiscence has in fact been the main character used in the tribal classification of Bignoniaceae (e.g., Don, 1838; de Candolle, 1845; Bureau, 1864; Schumann, 1894; Gentry, 1992c), although anatomical and ontogenetic study is still needed to determine if fruit dehiscence is indeed a

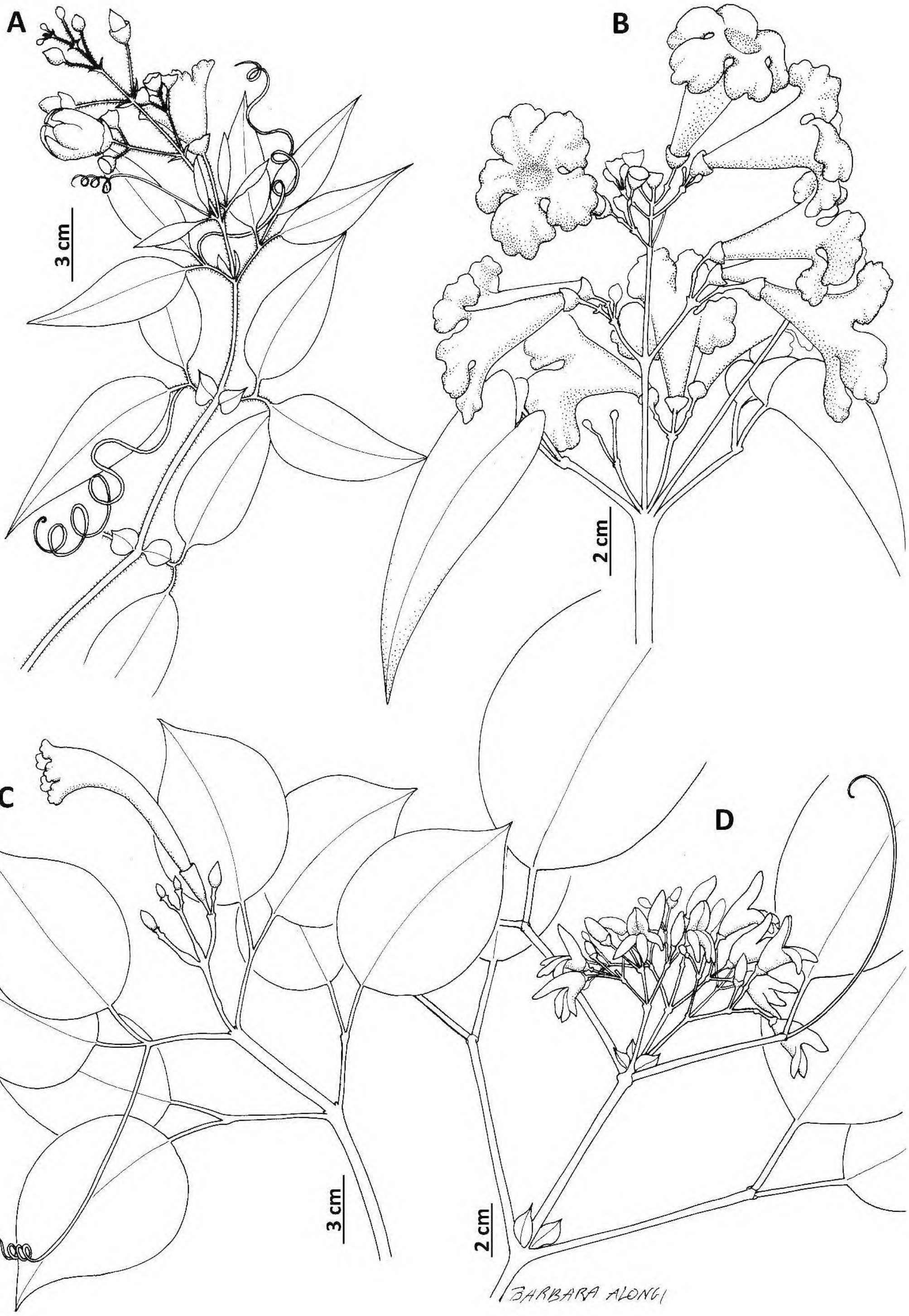


Figure 10. Morphological diversity in *Bignonia* L. —A. Flowering branch of *Bignonia campanulata* Cham. (this species was previously included in *Clytostoma* Miers ex Bureau). —B. Flowering branch of *B. aequinoctialis* L. (previously in *Cydista* Miers). —C. Flowering branch of *B. nocturna* (Barb. Rodr.) L. G. Lohmann (previously in *Tanaecium* Sw.). —D. Flowering branch of *B. prieurii* DC. (previously in *Mussatia* Bureau ex Baill.). A illustrated from *Lombardi 2526* (MO); B from *Gillespie & Persaud 1198* (MO); C from *Cogollo & Cardenas 4480* (MO); D from *Schunke 5010* (MO).

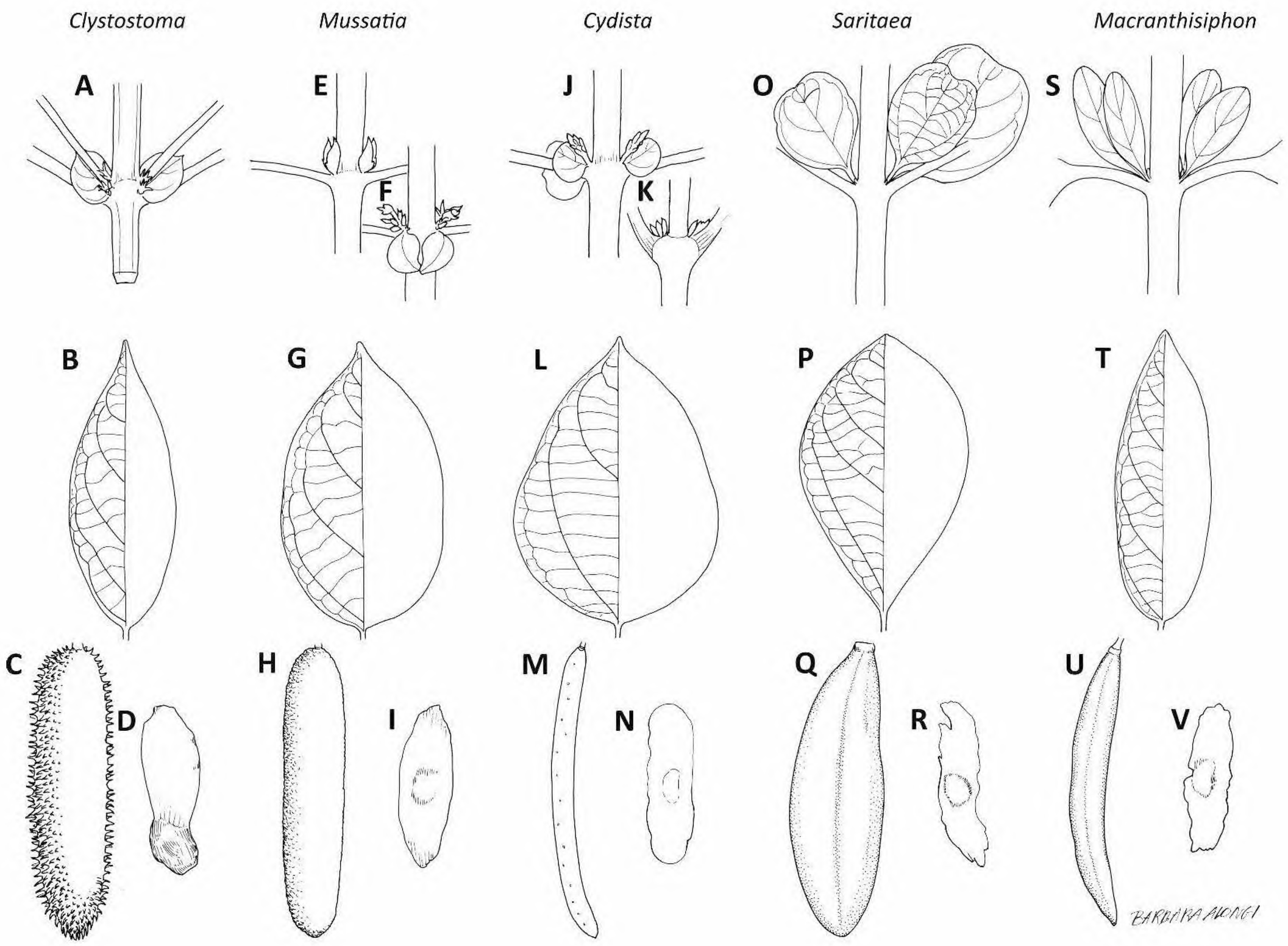


Figure 11. Comparison of prophylls of the axillary buds (top row), leaves, and fruits (lower two rows), with seeds seen to right of fruits, among different species of *Bignonia* L.; names above columns indicate the genera in which these species were previously included. A–D. *Bignonia campanulata* Cham. E–I. *Bignonia hyacinthina* (Standl.) L. G. Lohmann. J–N. *Bignonia aequinoctialis* L. O–R. *Bignonia magnifica* W. Bull. S–V. *Bignonia longiflora* Cav. A–D illustrated from *Hoehne 3773* (MO); E–G from *Schunke 5010* (MO); H, I from *Saldias et al. 2934* (MO); J–N from *McDaniel 11860* (MO); O, P from *Gentry et al. 15454* (MO); Q, R from *Cuadros et al. 3446* (MO); S–V from *Hansen et al. 7978* (MO).

character that diagnoses large clades within the family (Olmstead et al., 2009). Within the tribe Bignonieae fruit shape and ornamentation are among the least stable characters, even though they have been commonly used to delimit genera in previous classification systems. This together with the similar variation in corolla form and color explain in large part why previous classifications of Bignonieae have been unstable and phylogenetically unsatisfactory. The only fruit character that is unique to a single clade of Bignonieae is the 4-parted arrangement of the mature fruit valves in *Dolichandra*, versus 2-parted in the other members of the tribe.

Seed coat. The seed coat or surface is smooth in most of the Bignonieae (Fig. 4A). However, the seeds are papillate to pubescent in *Amphilophium* (Fig. 4C, D), and this condition is a synapomorphy for the genus. In addition, the seeds are rough in *Neojobertia* (Fig. 4B) and *Xylophragma*.

Taxonomic Treatment

The new generic classification of Bignonieae here is based on both morphological and molecular study of this group, as summarized above and detailed elsewhere (Lohmann, 2003, 2006; Lohmann et al., in prep.). The names and relationships of the genera recognized here are shown in the schematic phylogeny presented in Figure 2. A modified natural key is given here to the genera, following this schematic phylogeny: somewhat differently from an artificial key, the main purpose of this natural key is to outline the characters and relationships of the clades or natural groups. In this key, the leads summarize the characterization of each of the genera being separated in the order in which they appear on the phylogeny; therefore, sometimes some of the cited character states are not completely exclusive in contrasting leads of a couplet. For further insights into the identification of genera see Tables 3 and 4. The taxonomic treatment of the individual genera details their component species. In the morphological

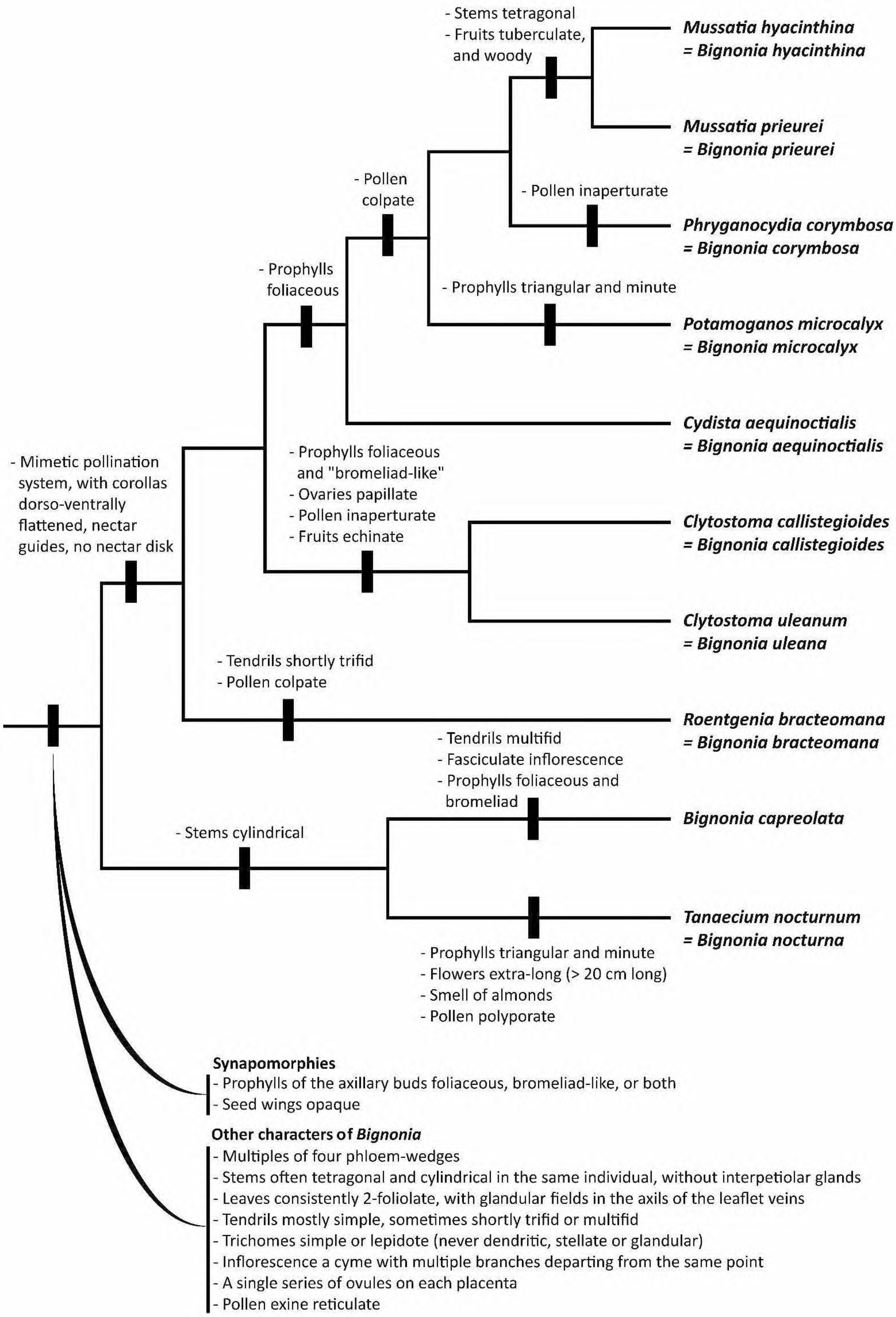


Figure 12. Phylogenetic hypothesis of *Bignonia* L. with morphological characters mapped on the diagram. Names of the terminal taxa indicate the genera in which these species were previously included and changes in the classification proposed here are indicated. The synapomorphies represent unique characters that diagnose the genus; the other characters are found in *Bignonia* and additionally describe the genus. Relationships depicted follow Lohmann (2006).

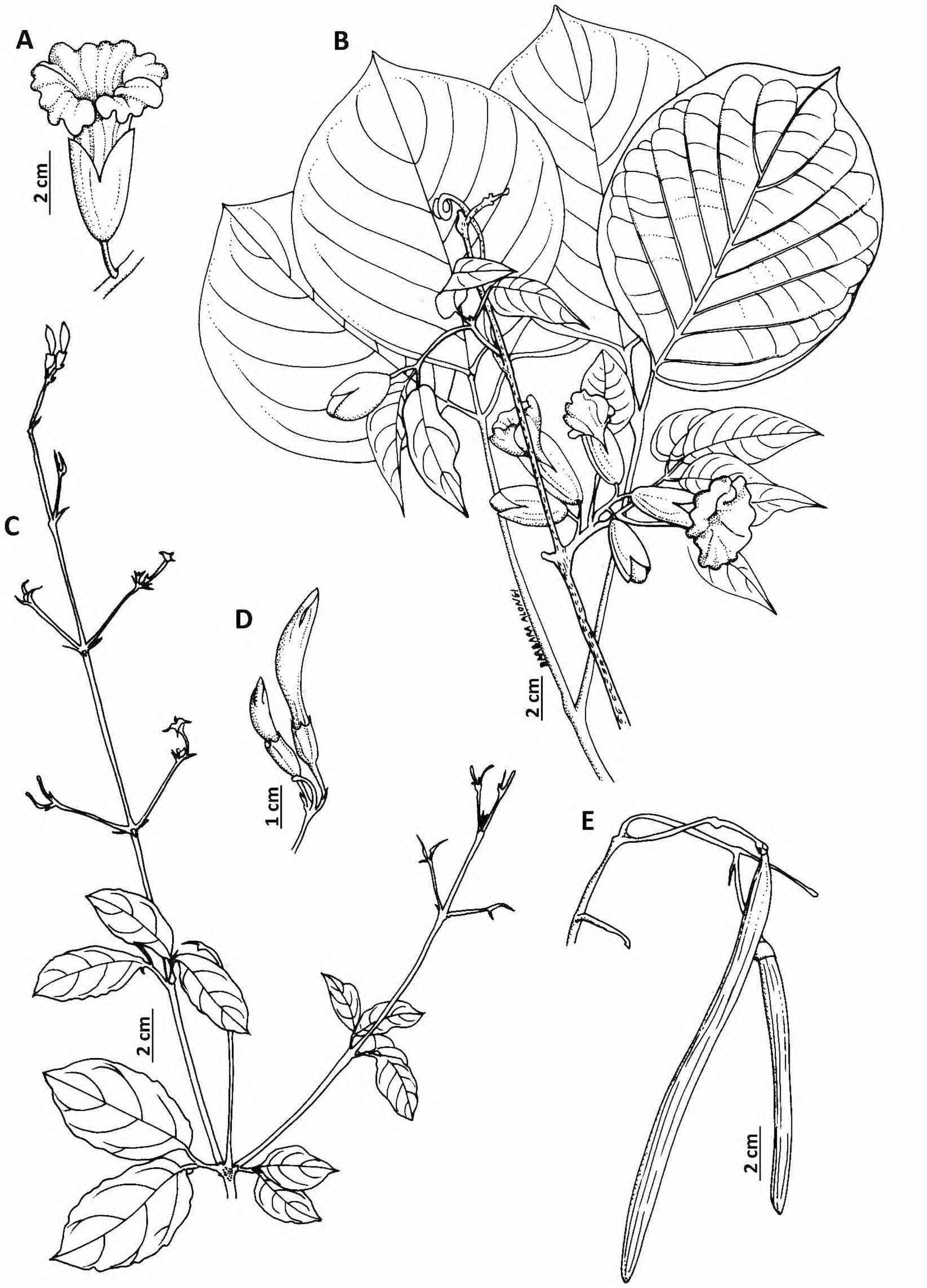


Figure 13. Representative morphological traits of *Callichlamys* Miq. and *Cuspidaria* DC. A, B. *Callichlamys latifolia* (Rich.) K. Schum. —A. Flower. —B. Flowering branch. C–E. *Cuspidaria cinerea* (Bureau ex K. Schum.) L. G. Lohmann. —C. Flowering branch. —D. Flower buds. —E. Fruits. A, B illustrated from *Costa et al. 211* (MO); C–E from *Lohmann et al. 34* (MO).

descriptions, the character states noted in parentheses are rarely occurring ones. The list of the species of Bignonieae here summarizes the current knowledge of the group, and forms the basis for monographic studies of this tribe (Lohmann, 2003; Lohmann et al., in prep.).

All accepted names are listed here, and in a few cases also synonyms that clarify past confusions, clarify changes of names for well-known species, or represent revised species circumscriptions used here. Presentation of full synonymy is beyond the scope of this work; most of this synonymy can be found in iPlants (<http://www.iplants.org/>). In general, invalid names are not cited here, except in several cases where these have been widely used and have generated nomenclatural confusion. The nomenclatural discussions and citations of particular Articles of the International Code of Botanical Nomenclature are based on McNeill et al. (2006). Formal nomenclatural author and reference abbreviations follow usage in TROPICOS®, and herbarium acronyms follow Index Herbariorum (<http://sweetgum.nybg.org/ih/>). The genera are treated here in alphabetical order, and within each genus, the species are treated in alphabetical order. Specimen data and images of living plants and representative specimens can be found in TROPICOS® (<http://www.TROPICOS.org/>), which includes A. H. Gentry's specimen database and photographs. The geographic range information given here is intended to generally describe the species distributions and is based on literature plus a georeferenced dataset that includes 30,000 specimen records (Lohmann, unpubl. data). Maps illustrating the distributions of representative species have been published elsewhere (Lohmann et al., 2013), and maps for the remaining taxa based on georeferenced specimens can be obtained upon request from the first author. Countries with relatively small surface areas are listed individually; for countries with larger areas, the main political units (states, provinces, or departments) in which the species are documented are also detailed.

Types were examined for most of the species treated here. Typification of the names treated here is done as far as possible, but typification of all names is beyond the scope of the present work. Typification is done here in particular for names published by Vellozo, Jacquin, Bureau, and Schumann. The lectotypification and neotypification here are all done by L. G. L., and should be credited solely to her.

Vellozo (1825 [1829], 1827 [1831]; also spelled Velloso or Veloso, Stafleu & Cowan, 1986) described and illustrated many new genera and species in his treatment of the Bignoniaceae in his *Flora Fluminensis*. Most of Vellozo's names were based on his own collections from southern Brazil, mainly Rio de Janeiro and Minas Gerais, which were deposited at the herbarium R in Rio de Janeiro. These specimens are apparently all lost (Stafleu & Cowan, 1986: 697), making the plates from *Flora Fluminensis* the only existing authentic materials of Vellozo. Gentry (1975) reviewed Vellozo's Bignoniaceae names and confirmed their identities in modern taxonomy, but did not lectotypify them. Vellozo's plates are here designated as lectotypes for several of his names, following recommendations by Ross (2002).

Jacquin also did not designate types for several of the taxa that he described, making lectotypification necessary. Whenever Jacquin mentioned that his description was based on his own collection from a particular locality, lectotypes or neotypes have usually not been designated here. For these names the types are here provisionally designated as *Jacquin s.n.* pending further study, unless original materials have already been traced. Jacquin's original specimens do survive in many cases and are often deposited at BM or W, with specimens also dispersed among various European herbaria (Stafleu & Cowan, 1979: 407), so locating this material is feasible but difficult. In addition, several species described by Jacquin were based on specimens of other collectors (D'Arcy, 1970). In some cases Jacquin made no reference to materials that he examined and his plates are here designated as lectotypes.

Chamisso (1832) stated that his treatment of the Bignoniaceae was based on the collections of Friedrich Sellow (also spelled Sello, Stafleu & Cowan, 1985) from Brazil, but he gave no collection numbers for the specimens that he cited. Several numbered specimens of Sellow's collections were photographed at the Berlin Museum (B) in the Field Museum's type photograph series, because these were catalogued as types of various Bignonieae species that Chamisso described. These and other Sellow duplicates distributed to various herbaria help confirm the identity of Chamisso's names, and when the Field Museum photo confirms that the B specimen represents the correct species, that specimen number is presumed to be the type number. However, Chamisso's original herbarium is deposited at LE (Stafleu & Cowan, 1976: 482) and is presumed to contain the holotypes of his names (unless the name was specifically based on a specimen deposited elsewhere). It may eventually be necessary to lectotypify some of Chamisso's names, but this cannot be done until the Bignonieae types of the

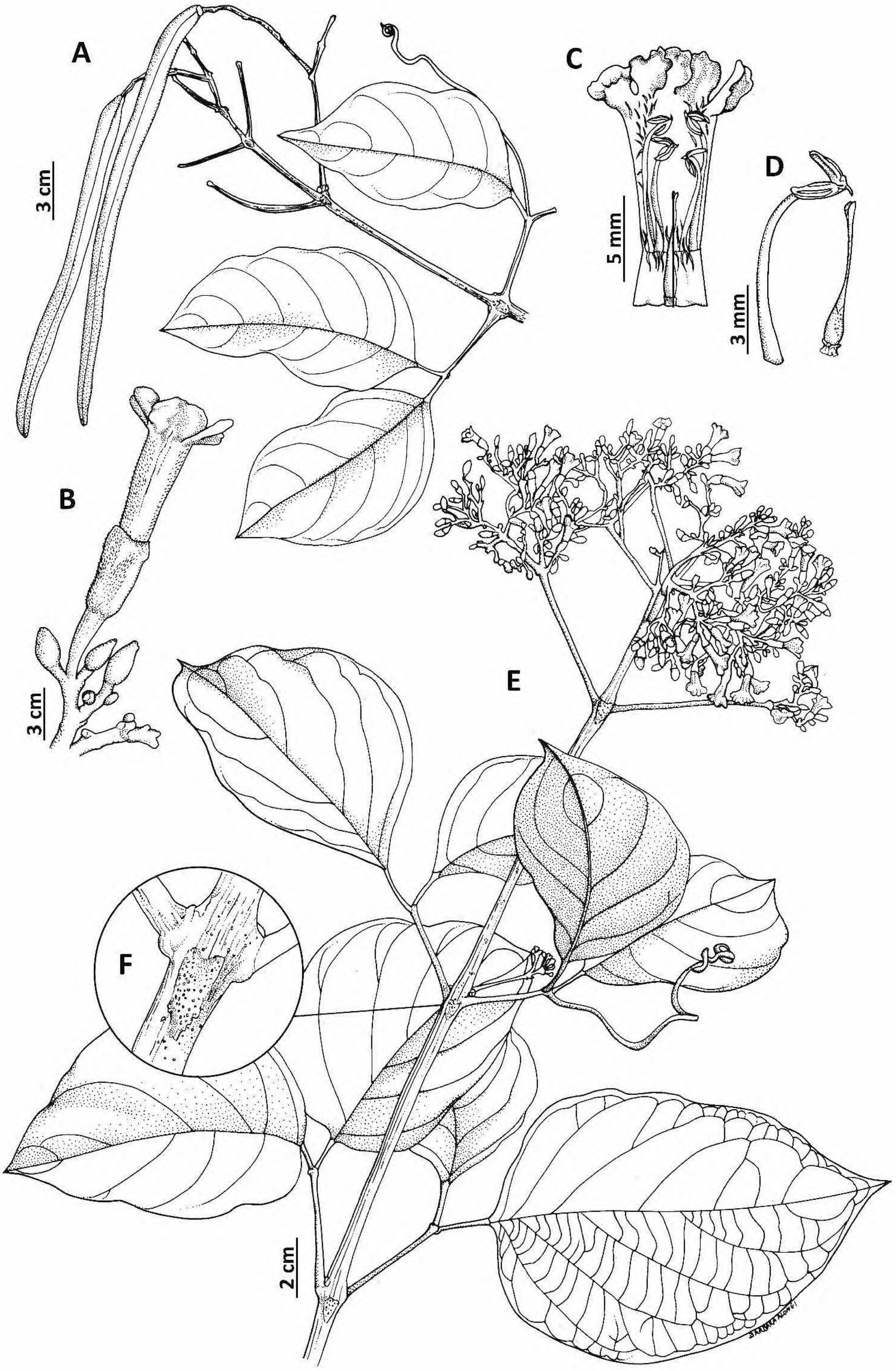


Figure 14. Representative morphological traits of *Fridericia* Mart. A–F. *Fridericia trailii* (Sprague) L. G. Lohmann. —A. Fruiting branch. —B. Flower and flower buds. —C. Opened flower. —D. Stamen and gynoecium, with the gynoecium at right. —E. Flowering branch. —F. Detail of the interpetiolar glands. A illustrated from *Costa et al. 65* (MO); B–F from *Lohmann et al. 29* (MO).

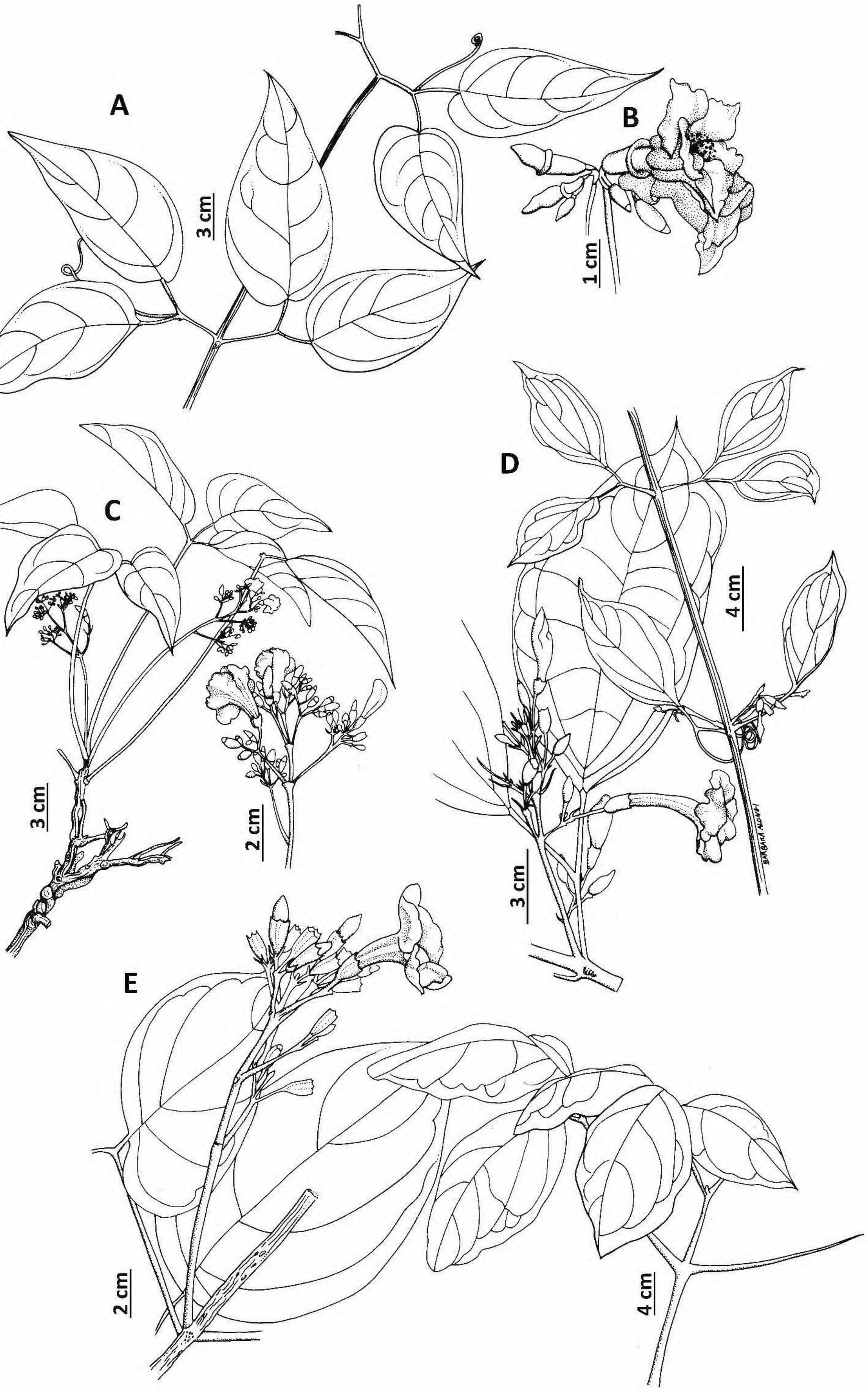


Figure 15. Morphological diversity in *Fridericia* Mart. A, B. *Fridericia triplinervia* (Mart. ex DC.) L. G. Lohmann. —A. Branch. —B. Flowers. —C. *Fridericia chica* (Bonpl.) Verl., flowering branch and flowers. —D. *Fridericia prancei* (A. H. Gentry) L. G. Lohmann, flowering branch. —E. *Fridericia nigrescens* (Sandwith) L. G. Lohmann, flowering branch. A, B illustrated from *Lohmann et al. 11* (MO); C from *Gentry 12816* (MO); D from *Sothers et al. 460* (MO); E from *Assunção et al. 430* (MO).

LE herbarium are studied; therefore Chamisso's names are not lectotypified here pending that work.

Schumann in his synoptic overview of the Bignoniaceae for the *Pflanzenfamilien* (1894) did not cite collections for any of the new species he described, but the Bignonieae species he named there were contemporaneously detailed by Bureau and Schumann (1896) in the *Flora Brasiliensis*. These two works were presumably prepared in close coordination, and the specimens cited by Bureau and Schumann are here considered to be original material of the species Schumann named in the *Pflanzenfamilien*. The general collection of Neotropical Bignoniaceae specimens at B was destroyed during World War II (Hiepko, 1987), which resulted in the loss of all of Schumann's original materials. These destroyed types are indicated in the text by the dagger symbol (†). Lectotypifications are made here when possible for names that were based on types lost there, but further study is necessary before this can be done in several cases.

Parts of this new classification have already been published, due to varying publication schedules in overlapping floristic works. In particular, several of the nomenclatural combinations supported by the phylogeny of Bignonieae (Lohmann, 2006) were previously cited by Arbo and Lohmann (2008) and Lohmann (2008a, 2008b, 2010) in regional checklists. The necessary new nomenclatural combinations were all intended to be published in the comprehensive classification here, and were cited in those regional checklists in anticipation of this present article but not in a form intended for valid publication. However, because of its format those new names were validly published by Lohmann (2008a), where all the nomenclatural requirements (McNeill et al., 2006) were met: the name was clearly accepted in the work (Art. 34.1), the new combination was explicitly and fully given (Art. 33.1), and the basionym was given with its place of publication (Art. 33.4). The names cited by these other works did not satisfy this last requirement and are not validly published.

Tribe Bignonieae Dumort., Anal. Fam. Pl. 23. 1829. (Bignoniaceae). TYPE: *Bignonia* L.

Lianas, shrubs, or rarely treelets, with juvenile growth infrequently dimorphic, glabrous or pubescent with various types of trichomes including simple, glandular, dendritic, lepidote, and stellate; stems generally with (without) anomalous secondary growth produced by atypical cambia forming 4 to 32 phloem wedges in various arrangements, with pith solid (hollow); branchlets cylindrical, tetragonal, or hexagonal in cross-section, with interpetiolar glands and/or an interpetiolar ridge sometimes present; prophylls of axillary buds minute and triangular, bromeliad-like, ensiform, foliaceous, or subulate, sometimes with glands. Leaves (1)2- or 3(or 5)-foliolate, biternately compound, or biternately pinnate, with terminal division often replaced by a simple, bifid, trifid, or multifid tendril, this with or without adhesive disks; leaflets frequently with glands, pellucid punctations, and/or domatia of various forms. Inflorescence terminal and/or axillary, a thyrse, compound thyrse, raceme, cyme, corymb, or fascicle. Flowers with calyx cupular, tubular, or urceolate, variously truncate, 2- to 5-lobed, spathaceous opening by a lateral slit, or calyptrate and circumscissile, sometimes appendaged, without or frequently with glands; corolla tubular to infundibuliform, white, yellow, cream, pink, magenta, orange, or red, lobes 5, in bud imbricate (valvate at base and imbricate at apex); stamens (2 or)4 with 1(no) posterior staminode, didynamous, thecae 2, parallel to divergent or forward-curved; ovary bilocular, with placentation axile, placentas 4, each with 1 to many ovules in varied arrangements; stigmas 2; nectar disk present (absent). Fruit capsular, septicidal, widely varied in form and ornamentation, valves 2(4); seeds smooth (rough or pubescent to papillose), winged (unwinged).

This tribe includes 21 genera with 393 species, all of them Neotropical except *Bignonia capreolata* L., which is found in the warm-temperate southeastern United States.

Natural Key to Genera of Tribe Bignonieae

1a. Leaves biternately compound, with leaf divisions never replaced by tendrils; petioles frequently becoming woody and twining ..... XV. *Perianthomega*

1b. Leaves 1- to 5-foliolate, biternately compound, or biternately pinnate, with terminal divisions often replaced by tendrils; petioles not twining, woody, or tendril-like (Fig. 2, node B).

2a. Leaves biternately compound or biternately pinnate; branchlets hexagonal in cross-section; tendrils trifid or multifid ..... XIII. *Neojobertia*

2b. Leaves 1- to 5-foliolate, biternately compound, or biternately pinnate, branchlets cylindrical, irregularly angled, or tetragonal, and tendrils simple or bifid, OR sometimes branchlets hexagonal in cross-section and then leaves 1- to 3-foliolate and tendrils trifid or multifid, OR sometimes tendrils trifid or multifid and then leaves 2- to 5-foliolate and branchlets cylindrical, irregularly angled, or tetragonal.

3a. Petioles articulated at stem and petiolules articulated at petioles; calyx and fruit with volcano-shaped glands ..... I. *Adenocalymma*

3b. Petioles and petiolules not articulated; calyx and fruit with patelliform or immersed glands (Fig. 2, node D).
4a. Stems with hollow pith; leaflets with pellucid punctations; fruits linear and narrow (i.e., less than 1 cm wide) ..... XVIII. *Stizophyllum*
4b. Stems with solid pith, or pith tardily becoming hollow in some species of *Pleonotoma*; leaflets generally without pellucid punctations, OR with pellucid punctations and then stems with solid pith; fruit elliptic to linear, more than 1.5 cm wide (Fig. 2, node E).
5a. Tendrils multifid with the segments ending in adhesive disks ..... X. *Manaosella*
5b. Tendrils simple, bifid, trifid, or multifid and without adhesive disks, OR with trifid and rarely multifid both found on the same plant and the segments ending in adhesive disks.
6a. Petioles tetragonal in cross-section; branchlets tetragonal in cross-section, with angles acute and winged; leaves biternately compound or biternately pinnate ..... XVI. *Pleonotoma*
6b. Petioles cylindrical in cross-section; branchlets cylindrical, tetragonal, or hexagonal in cross-section, without angles or with angles but these not winged; leaves 1- to 5-foliolate, OR if leaves biternately compound then branchlets cylindrical (Fig. 2, node G).
7a. Stems in cross-section with phloem wedges in multiples of 4, or with multiple dissected phloem wedges (Fig. 2, node H).
8a. Stems in cross-section with multiple dissected phloem wedges; tendrils trifid with uncinate tips; fruit incompletely to completely 4-parted ..... VII. *Dolichandra*
8b. Stems in cross-section with multiples of 4 phloem wedges; tendrils simple, bifid, trifid, or multifid, with tips not uncinate; fruit 2-parted (Fig. 2, node I).
9a. Juvenile growth dimorphic; tendrils with segments terminating in adhesive disks; corolla coriaceous; fruit elliptic, with valves woody; seeds pubescent or papillate ..... II. *Amphilophium*
9b. Juvenile growth similar to adult, or dimorphic in one species of *Mansoa*; tendrils without adhesive disks; corolla membranaceous; fruit linear or elliptic, with valves woody or coriaceous; seeds glabrous and smooth (Fig. 2, node J).
10a. Prophylls of the axillary buds foliaceous and bromeliad-like or minute and triangular; tendrils simple, minutely trifid, or multifid; calyx coriaceous; and seed wings opaque ..... IV. *Bignonia*
10b. Prophylls of the axillary buds triangular and minute, elliptic and foliaceous, and/or bromeliad-like; tendrils simple or trifid; calyx coriaceous or membranaceous; and seed wings opaque, hyaline, or absent, with characters not found in the above combination (Fig. 2, node K).
11a. Branchlets cylindrical, becoming angled to ribbed; foliage with strong garlic odor; corolla magenta; ovary glabrous or villose; pollen exine areolate; fruits woody, with midrib frequently developed into a conspicuous ridge, with calyx caducous ..... XI. *Mansoa*
11b. Branchlets cylindrical and smooth; foliage without garlic odor; corolla red, orange, yellow, or cream; ovary lepidote; pollen exine reticulate; fruits coriaceous, not ridged, with calyx persistent (Fig. 2, node L).
12a. Branchlets cylindrical in cross-section; prophylls of axillary buds elliptic and foliaceous or minute and triangular, with glands; leaflets without pellucid punctations; inflorescence a raceme, fascicle, cyme, or compound thyrse; corolla infundibuliform, white, yellow, or red, with glands arranged in lines, the lobes with complete imbricate aestivation; stamens included; ovules in multiple series on each placenta; fruit elliptic and stipitate ..... III. *Anemopaegma*
12b. Branchlets hexagonal in cross-section; prophylls of axillary buds minute and triangular, without glands; leaflets with pellucid punctations; inflorescence a corymb; corolla narrowly tubular, orange or white, without glands, the lobes with valvate aestivation at their bases and imbricate aestivation at their apices; stamens exserted; ovules biseriate on each placenta; fruit linear and without stipe ..... XVII. *Pyrostegia*
7b. Stems in cross-section with 4 phloem wedges (Fig. 2, node M).
13a. Calyx spathaceous and spongy ..... V. *Callichlamys*

13b. Calyx cupular, urceolate, or tubular and 2- to 5-parted, truncate, spathaceous, or calyptrate, membranaceous to coriaceous but not spongy (Fig. 2, node N).
14a. Branchlets with a continuous ring-shaped ridge surrounding the interpetiolar region; calyx irregularly 3- to 4-lobed ..... XII. *Martinella*
14b. Branchlets without interpetiolar ridges or with discontinuous interpetiolar ridges; calyx bilabiate, 5-lobed, truncate, or spathaceous (Fig. 2, node O).
15a. Older branchlets with papery peeling epidermis or bark; calyx with glands arranged in a line ..... XIV. *Pachyptera*
15b. Older branchlets with smooth, non-peeling epidermis or bark; calyx without glands, with solitary glands near margins, or with glands clustered in fields near margins (Fig. 2, node P).
16a. Calyx bilabiate; prophylls of axillary buds subulate and/or bromeliad-like ..... XIX. *Tanaecium*
16b. Calyx truncate, bilabiate, 5-parted, spathaceous, or calyptrate; prophylls of axillary buds minute and triangular, foliaceous, or bromeliad-like (Fig. 2, node Q).
17a. Prophylls of axillary buds foliaceous or minutely triangular, without or with glands; foliage with clove odor; corolla less than 2 cm long, strongly bilabiate . . . . XX. *Tynanthus*
17b. Prophylls of axillary buds minutely triangular or bromeliad-like, without glands; foliage without clove odor; corolla more than 4 cm long, not bilabiate.
18a. Calyx truncate, shortly 5-parted, calyptrate (i.e., splitting transversally), without glands; ovary, anthers, and stigma pubescent; nectar disk absent . . .. IX. *Lundia*
18b. Calyx truncate or deeply 5-parted, lobed (i.e., splitting longitudinally), with glands; ovary lepidote, anthers and stigma glabrous; nectar disk present.
19a. Ovules arranged in 2 series on each placenta; anthers with thecae forward-curved; fruit valves with midrib divided into 2 longitudinal ridges ..... VI. *Cuspidaria*
19b. Ovules arranged in 1 or multiple series on each placenta; anthers with thecae straight, OR thecae forward-curved and ovules arranged in 1 series on each placenta; fruit valves not ridged (Fig. 2, node R).
20a. Ovules arranged in a single series on each placenta ..... VIII. *Fridericia*
20b. Ovules arranged in multiple series on each placenta ..... XXI. *Xylophragma*

I. Adenocalymma Mart. ex Meisn., Pl. Vasc. Gen. 1: 300, 2: 208. 1840, orth. cons. vs. *Adenocalymna*, emend. L. G. Lohmann. TYPE: *Adenocalymma comosum* (Cham.) DC. (lectotype, designated by Sandwith [1962: 453]).

Memora Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. TYPE: *Memora schomburgkii* (DC.) Miers (lectotype, designated by Sandwith [1962: 454]) [≡ *Adenocalymma schomburgkii* (DC.) L. G. Lohmann].

Pharseophora Miers, Proc. Roy. Hort. Soc. London 3: 186. 1863, syn. nov. TYPE: *Pharseophora fallax* (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 186. 1863, nom. superfl. illeg. [= *Adenocalymma pubescens* (Spreng.) L. G. Lohmann].

Odontotecoma Bureau & K. Schum., Fl. Bras. 8(2): 305. 1897. TYPE: *Odontotecoma fulgens* Bureau & K. Schum. [= *Adenocalymma cymbalum* (Cham.) Bureau & K. Schum.].

Sampaiella J. C. Gomes, Rodriguésia 12: 107. 1949, syn. nov. TYPE: *Sampaiella trichoclada* (DC.) J. C. Gomes [≡ *Adenocalymma trichocladum* (DC.) L. G. Lohmann].

Lianas or shrubs, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, glabrous to pubescent, covered with lenticels, without interpetiolar glands (with glands in *Adenocalymma trichoclada*), with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds small and subulate or well developed and foliaceous, with glands. Leaves 2- or 3-foliolate, biternately compound, or biternately pinnate, terminal leaflet or division often replaced by a simple (trifid) tendril, tendrils with adhesive disks, without uncinate apices; leaflets coriaceous

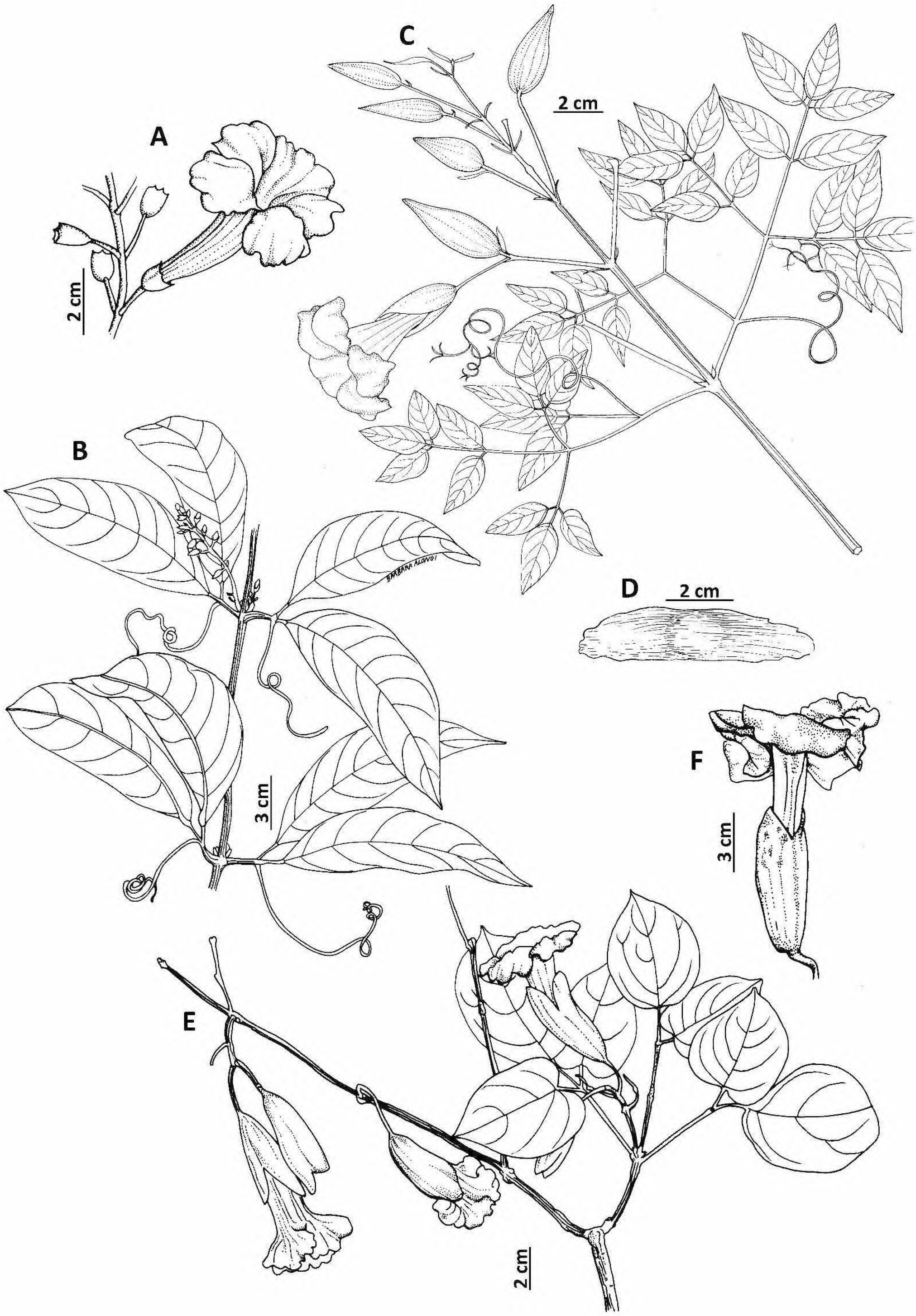


Figure 16. Representative morphological traits in *Mansoa* DC., *Neojobertia* Baill., and *Manaosella* J. C. Gomes. A, B. *Mansoa alliacea* (Lam.) A. H. Gentry. —A. Flower. —B. Flowering branch. C, D. *Neojobertia candolleana* (Mart. ex DC.) Bureau & K. Schum. —C. Flowering branch. —D. Seed. E, F. *Manaosella cordifolia* (DC.) A. H. Gentry. —E. Flowering branch. —F. Flower. A, B illustrated from *Vicentini et al. 672* (MO); C, D from *Gentry et al. 50136* (MO); E, F from *de Souza et al. 81* (MO).

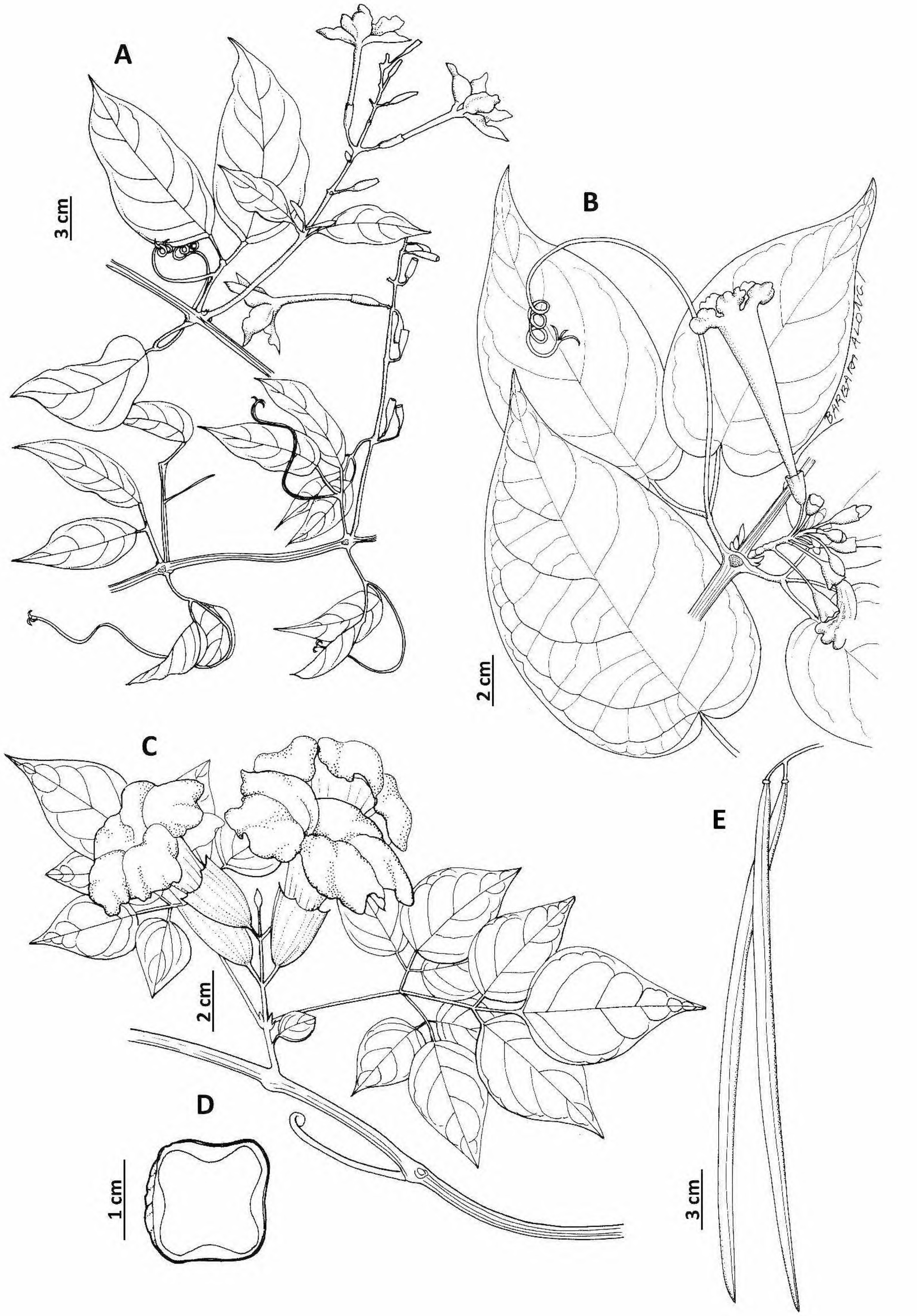


Figure 17. Representative morphological traits in *Pachyptera* DC. ex Meisn. and *Perianthomega* Bureau ex Baill. —A. *Pachyptera aromatica* (Barb. Rodr.) L. G. Lohmann, flowering branch. —B. *Pachyptera kerere* (Aubl.) Sandwith, flowering branch. C–E. *Perianthomega vellozoi* (Vell.) Bureau. —C. Flowering branch. —D. Cross-section of stem. —E. Fruit. A illustrated from *Lohmann et al. 28* (MO); B from *Weitzman & Hahn 287* (MO); C from *Coimbra 743* (MO); D from *Gentry et al. 73603* (MO); E from *Michel et al. 424* (MO).

(membranaceous), with (without) glands, without pellucid punctations, without domatia, petiolules articulated; petiole cylindrical, never modified into a tendril, articulated. Inflorescence axillary and/or terminal, a raceme (thyrse in *A. trichoclada*). Flowers zygomorphic, pentamerous; calyx cupular, shortly 5-lobed, 5-apiculate, or bilabiate, coriaceous, glabrous to villose externally, with volcano-shaped glands clustered near margins; corolla bright yellow (red, white), without nectar guides, infundibuliform (urceolate), straight in tube, membranaceous, puberulous (villose) externally, with glands on upper portion of tube, lobes 5, imbricate; stamens 4, with well-developed filaments, included (exserted), anthers glabrous, thecae straight, pollen in monads, inaperturate (colpate), with exine reticulate; ovary sessile, smooth and lepidote externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear or elliptic, flattened to inflated, straight, woody or coriaceous, with valves 2(4), glabrous to villose, without lenticels, with volcano-shaped glands, without wings, smooth or with midrib sometimes developed into a prominent ridge, with calyx caducous; seeds winged or corky and wingless, with seed body smooth and glabrous, wings linear, hyaline or opaque. Figure 5.

Nomenclatural note. The Martius material on which the name *Tecoma fulgens* Mart. is based is apparently a mixed collection of two species that are now called *Adenocalymma cymbalum* and *A. schomburgkii* (DC.) L. G. Lohmann. The application of the name *T. fulgens* has generally (e.g., Bureau & Schumann, 1896) followed the usage of de Candolle (1845), in which the name *T. fulgens* applies to the plants now called *A. cymbalum*, and the specimen of *T. fulgens* at G-DC (image!) clearly represents *A. cymbalum*. Further study of the Martius type material is needed, but for now the name *T. fulgens* is here considered a synonym of *A. cymbalum*.

Number of species, distribution, and habitat. *Adenocalymma* includes 82 species found in wet to dry forest, caatinga, and cerrado vegetation from Mexico and the Lesser Antilles to Paraguay and southeastern Brazil.

Memora, *Pleonotoma*, and *Pharseophora* were described by Miers (1863) based on species that all had biternately pinnate leaves, but differed in flower color. The affinities between *Memora* and *Adenocalymma* were noted by Bentham (1876), who put *Memora* in synonymy with *Adenocalymma*, but this classification was rejected by subsequent workers on Bignonieae. Even though Gentry and Tomb (1979: 766) noted the affinities between *Adenocalymma* and *Memora*, they maintained them as separate based on a distinction between the "usually pinnate" leaves of *Memora* and the 2- or 3-foliolate leaves of *Adenocalymma*. Gentry and Tomb noted (1979: 766) that "*Memora* could readily be merged with *Adenocalymma* if the not-always-constant definitive character of pinnately compound versus 3-foliolate or 2-foliolate leaves were neglected." Indeed, the biternately pinnate leaves of *Memora* (sometimes also called pinnate or 2- to 3-ternately compound) vary within some species, and even on an individual plant (e.g., *M. bracteosa*). The discovery of the species *M. tanaeciicarpa* A. H. Gentry, which is morphologically intermediate between the two genera, added to the confusion over delimitation of these genera. Gentry noted (1976: 58) about *M. tanaeciicarpa*: "This is quite unlike any other species of *Memora* in its large 4-valved capsule, its puberulous style and ovary, its yellowish-red puberulous 5-denticulate calyx, and its puberulous corolla tube. Except for the 2- or 3-ternately compound leaves it seems closer to *Adenocalymma comosum* and allies than to other *Memora* species, additional evidence of the artificiality of the separation of *Memora* and *Adenocalymma*."

Despite limited sampling of the *Memora–Sampaiella–Adenocalymma* clade for the molecular phylogeny (12 species out of 82), the current analysis suggests strongly that *Memora*, although monophyletic, is nested inside *Adenocalymma*. *Memora* and *Adenocalymma* share several distinctive features: stems with four phloem wedges in cross-section; strongly swollen, woody nodes; subwoody and strongly articulated petioles and petiolules; glandular, foliaceous prophylls; racemose inflorescences; yellow to red, pubescent corollas; ovules arranged in a single series on each placenta; inaperturate, reticulate pollen; and the unique volcano-shaped glands found on the calyx and fruit (Fig. 3). The affinities between *Adenocalymma* and *Sampaiella* are, however, less obvious and their close relationship has not been proposed on the basis of morphology alone. Previous studies considered *Sampaiella* closely related to *Arrabidaea* and *Cuspidaria* (e.g., Silva-Castro et al., 2004) based on the shared cymose inflorescences and colpate pollen, neither of which is found in *Adenocalymma* s. str. However, *Sampaiella* is well supported by molecular data as embedded within *Adenocalymma* (Lohmann, 2006) and also has volcano-shaped glands. Therefore *Adenocalymma* is here circumscribed to include *Memora* and *Samapiella*, and the volcano-shaped glands are a synapomorphy of this group. Most

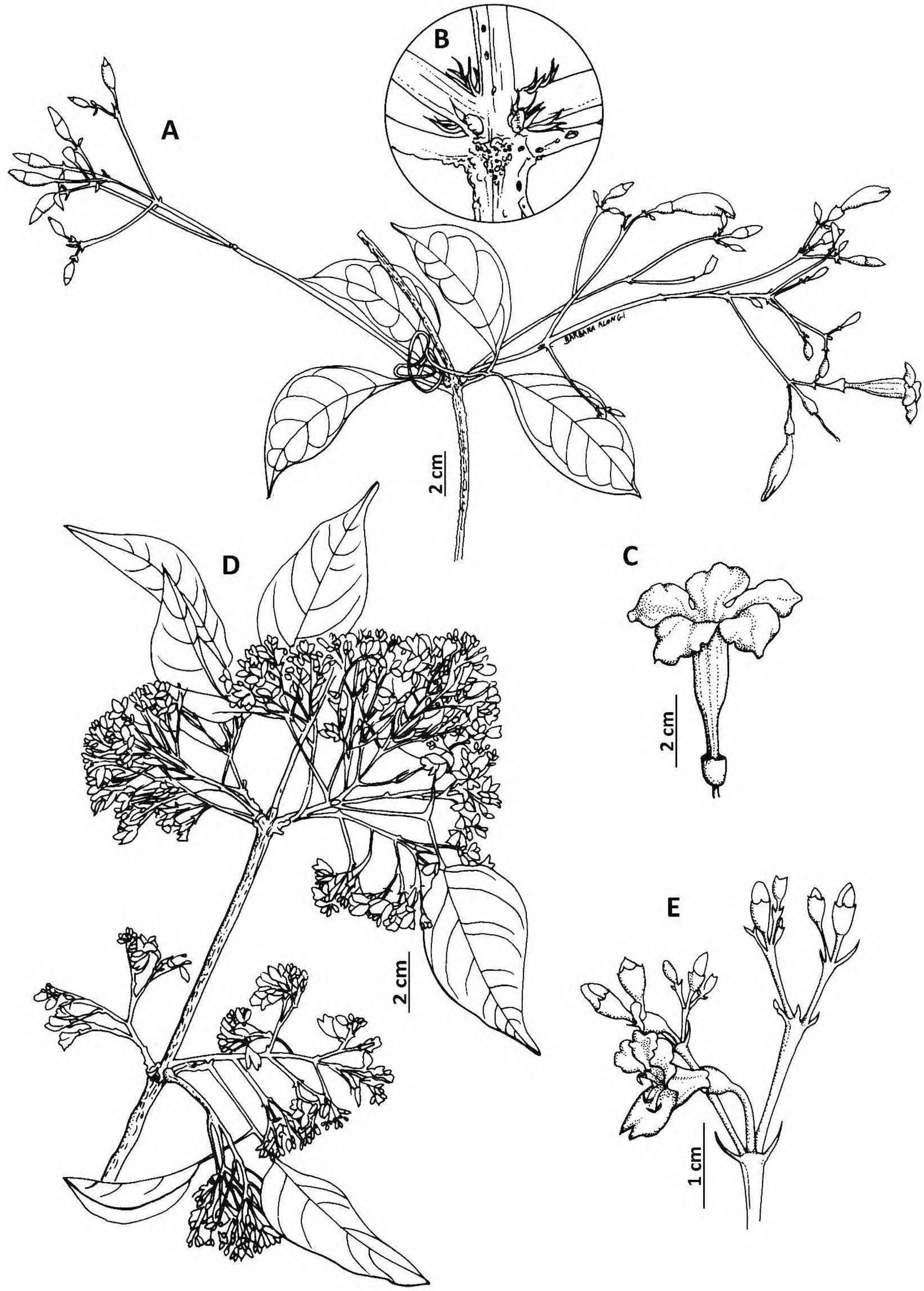


Figure 18. Representative morphological traits in *Tanaecium* Sw. and *Tynanthus* Miers. A–C. *Tanaecium truncatum* (A. Samp.) L. G. Lohmann. —A. Flowering branch. —B. Prophylls of axillary buds. —C. Flower. D, E. *Tynanthus panurensis* (Bureau) Sandwith. —D. Flowering branch. —E. Flower and flower buds. A–C illustrated from *Lohmann et al. 33* (MO); D, E from *Procópio et al. 14* (MO).

Adenocalymma species are pollinated by bees, a few by hummingbirds (Gentry, 1990).

As noted by Vizoni (2000), the spelling of the genus name *Adenocalymma* has varied. The name is a compound of two Greek words, "adenos," meaning "glands," and "kalymma," meaning "head covering." The spelling Adenocalymma has been conserved over Adenocalymna (McNeill et al., 2006).

1. Adenocalymma adenophorum (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Memora adenophora* Sandwith, Kew Bull. 13: 435. 1958 [1959]. *Adenocalymma adenophorum* (Sandwith) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 758. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus, BR-17, Km. 11, 16 Apr. 1956, *J. Chagas 3734* (holotype, K!; isotype, INPA-3734!).

Habitat and distribution. This species is restricted to wet forest vegetation in the area of Manaus in north-central Brazil (Amazonas).

2. Adenocalymma album (Aubl.) L. G. Lohmann, comb. nov. Basionym: *Bignonia alba* Aubl., Hist. Pl. Guiane 2: 653, tab. 266. 1775. *Jacaranda alba* (Aubl.) Spreng., Syst. Veg. 2: 834. 1825. *Memora alba* (Aubl.) Miers, Proc. Roy. Soc. London 3: 185. 1863. TYPE: French Guiana. Rivière Sinnamary, 25 leagues above mouth, s.d., *J. B. C. F. Aublet s.n.* (holotype, BM!, BM as photocopy at MO-2300309!).

Habitat and distribution. This species is restricted to riverine habitats in French Guiana.

3. Adenocalymma allamandiflorum (Bureau ex K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Memora allamandiflora* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 225. 1894. *Adenocalymma allamandiflorum* (Bureau ex K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 758. 2010, nom. nud. invalid. TYPE: Brazil. Pará: Santarém, June 1850, *R. Spruce 715* (holotype, M-86272!, M as photo F neg. 20472 at MO-1692999!; isotypes, BM-551288!, NY-313129!, P [barcode] P00481558!).

Habitat and distribution. This species is found in humid forest vegetation in Brazil (Amapá, Maranhão, Minas Gerais, Pará).

4. Adenocalymma apparicianum J. C. Gomes, Arch. Jard. Bot. Rio de Janeiro 9: 223. 1949. TYPE: Brazil. Ceará: Rd. betw. Fortaleza & Crato, 2 Aug. 1948, *A. P. Duarte 1249* (holotype, RB-68294!; isotypes, HUEFS not seen, K!, SPF-193216!).

Habitat and distribution. This species is found in dry caatinga vegetation in northeastern Brazil (Ceará, Rio Grande do Norte).

5. Adenocalymma apurense (Kunth) Sandwith, Lilloa 3: 461. 1938. *Bignonia apurensis* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 138. 1818 [1819]. TYPE: Venezuela. Apure: El Diamante, Apure River, s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland 812* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39410 at MO-1692916!; isotypes, B-W-11432!, K!).

Habitat and distribution. This species with water-dispersed seeds is found in humid lowland forest vegetation (Gentry, 1997) in Costa Rica, Panama, and Venezuela (Apure, Bolívar).

6. Adenocalymma arthropetiolatum A. H. Gentry, Ann. Missouri Bot. Gard. 60(3): 789, fig. 1E. 1973 [1974]. TYPE: Panama. Canal Zone [Colón]: Pipeline rd., 11 Nov. 1971, *A. H. Gentry 2460* (holotype, MO-2195517!; isotypes, F-2109794 image!, MO 2195518!).

Habitat and distribution. This species is restricted to wet forest vegetation in eastern Panama and Colombia (Antioquia, Chocó).

7. Adenocalymma aspericarpum (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Memora aspericarpa* A. H. Gentry, Ann. Missouri Bot. Gard. 61(3): 55, fig. 3. 1976. TYPE: Venezuela. Yaracuy: betw. Aroa & Altamira, 1050 m, 22 Jan. 1972, *J. A. Steyermark 105375* (holotype, MO-2097929!; isotype, VEN not seen).

Habitat and distribution. This species is found in wet lowland and premontane vegetation in Colombia (Antioquia, Caldas, Córdoba, Cundinamarca, La Guajira, Magdalena), Venezuela (Aragua, Barinas, Bolívar, Lara, Mérida, Miranda, Portuguesa, Táchira, Yaracuy, Zulia), and perhaps Peru (Loreto).

8. Adenocalymma axillare (K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Memora axillaris* K. Schum., Pflanzenfam. 4(3b): 225. 1894. *Adenocalymma axillare* (K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 758. 2010, nom. nud. invalid. TYPE: Brazil. Goiás: close to Trahiras, s.d., *J. E. Pohl 1882* (holotype, B†, B as photo F neg. 18442 at K! and at MO-1693000!;

lectotype, designated here, BR-876555!; isolectotypes, P [barcode] P00481557!, W [3]!).

Nomenclatural note. Two collections of this species were cited by Bureau and Schumann (1896), *Tamberlik s.n.* and Pohl's collection. The surviving specimen of these collections with the best material is here selected as the lectotype.

Habitat and distribution. This species is known from cerrado vegetation in Brazil (Goiás, Minas Gerais, Rondônia).

9. Adenocalymma bipinnatum (S. Moore) L. G. Lohmann, comb. nov. Basionym: *Macfadyena bipinnata* S. Moore, Trans. Linn. Soc. London, Bot. 4: 418. 1895. *Memora bipinnata* (S. Moore) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 43. 1976. *Adenocalymma bipinnatum* (S. Moore) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 758. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: ad Santa Cruz, Sep. 1891–1892, *S. Moore 290* (holotype, BM-573951!, BM as photocopy at MO-2300310!; isotype, MO-2300310!).

Habitat and distribution. This species is found in cerrado vegetation in eastern Bolivia and in Brazil (Goiás, Maranhão, Mato Grosso, Pará, Rondônia).

10. Adenocalymma biternatum (A. Samp.) L. G. Lohmann, comb. nov. Basionym: *Memora biternata* A. Samp., Anais Reunião Sul-Amer. Bot. 3: 169. 1938 [1940]. *Adenocalymma biternatum* (A. Samp.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 758. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Democracia, Madeira River, 30 Aug. 1923, *J. G. Kuhlmann 278* (holotype, RB-6464!; isotype, MO-2192034!).

Habitat and distribution. This species is found in forest vegetation in northern Bolivia and widely in Brazil (Amazonas, Rondônia, Mato Grosso, Pará).

11. Adenocalymma bracteatum (Cham.) DC., in A. DC., Prodr. 9: 200. 1845. *Bignonia bracteata* Cham., Linnaea 7: 692. 1832 [1833]. TYPE: Brazil. s. loc., s.d., *F. Sellow 1607* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18459 at MO-1692798!, K!).

Habitat and distribution. This species is found in wet to dry forest vegetation in Peru (Huánuco, Madre de Dios), Bolivia, Paraguay, and Brazil (Acre, Bahia, Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rondônia, São Paulo).

12. Adenocalymma bracteolatum DC., in A. DC., Prodr. 9: 200. 1845. TYPE: Bolivia. Chiquitos: Sanctae Annae, 1850, *A. d'Orbigny 758* (lectotype, designated here, P [barcode] P00468570!; isolectotypes, BR-880300!, G-DC!, G-DC as photo F neg. 26187 at K!, G-DC as photocopy at MO-1692799!, MO-3401782!, P [barcode] P00468571!, P [barcode] P00468572!, P [barcode] P00468573!, and P specimens without barcodes as photocopies at MO-2294595!, MO-2294596!, MO-2294597!, and MO-2294598!).

Nomenclatural note. De Candolle specifically cited a P specimen in the protologue of this name. Several duplicates of the type collection are deposited at P and the best sheet is here chosen as a lectotype.

Habitat and distribution. This species is found in wet forest vegetation in Peru (Madre de Dios), Bolivia, and Brazil (Bahia, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Rondônia, São Paulo).

13. Adenocalymma bracteosum (DC.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Spathodea bracteosa* DC., in A. DC., Prodr. 9: 208. 1845. *Pharseophora bracteosa* (DC.) Miers, Proc. Hort. Soc. London 3: 186. 1863. *Macfadyena bracteosa* (DC.) Benth., Gen. Pl. 2: 1035. 1876. *Memora bracteosa* (DC.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 226. 1894. TYPE: French Guiana. Cayenne, s.d., *Patris s.n.* (holotype, G-DC!, G-DC as photo F neg. 7691 at MO-1693058!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Chocó, Córdoba, Guainía), Venezuela (Amazonas, Apure, Barinas, Bolívar, Táchira), Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Maranhão, Pará).

14. Adenocalymma bullatum Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. TYPE: Brazil. Rio de Janeiro: près de Rezende, São José Vaz, 27 Sep. 1874, *A. Glaziou 7771* (lectotype, designated here, P!, P as photocopy at MO-2294588!; isolectotypes, B†, B as photo F neg. 18460 at MO-1692800!, K!, P not seen, P as photocopy at MO-2294589!, P not seen, P as photocopy at MO-2294590!).

Nomenclatural note. There are three duplicates of the type collection in Paris, where Bureau's original material is deposited. One of these was annotated as the holotype by P staff, based on knowledge of Bureau's work methods and original

materials, and this designation was accepted by Gentry in sched. (MO). Two other P sheets were annotated and accepted by Gentry in sched. as isotypes. However, this designation has been questioned and thus, to prevent confusion, this name is here lecotypified and the specimen previously considered the holotype is here chosen as the lectotype.

Habitat and distribution. This species is known from wet forest vegetation in southeastern Brazil (Rio de Janeiro).

15. Adenocalymma calcareum Udulutsch & P. Dias, Nordic J. Bot. 27(6): 459, figs. 1, 2. 2009. TYPE: Brazil. Rondônia: Presidente Médice, BR-364 hwy., 6.5 km of rd. to Alvorada do Oeste, from Presidente Médice to Vilhena, rd. to Embratel's hill, then 14 km, 11°15′58.8″S, 61°52′11.7″W, 222 m, 17 Nov. 2005, *R. G. Udulutsch & P. Dias 2668* (holotype, HRCB not seen; isotypes, MG not seen, SPF-178000!).

Habitat and distribution. This species is known from secondary vegetation in southwestern Brazil (Rondônia).

16. Adenocalymma campicola (Pilg.) L. G. Lohmann, comb. nov. Basionym: *Memora campicola* Pilg., Bot. Jahrb. Syst. 30: 195. 1901. *Adenocalymma campicola* (Pilg.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: s. loc., s.d., *R. K. F Pilger 677* (holotype, B†); Minas Gerais: Uberlândia, Estação Ecológica do Panga, Aug. 1998, *L. G. Lohmann & P. E. Oliveira 266* (neotype, designated here, SPF-195919!; isoneotypes HUFU-24939!, MO-5832449!).

Nomenclatural note. The type specimen of *Memora campicola* was destroyed at B. No isotypes have been found, so a neotype that has both flowers and fruits is designated here.

Habitat and distribution. This species is found in dry forest and savanna vegetation in central Brazil (Amazonas, Bahia, Goiás, Mato Grosso, Minas Gerais).

17. Adenocalymma chocoense A. H. Gentry, Phytologia 57: 240. 1985. TYPE: Panama. Darién: Ensenada del Guayabo, 16–19 km SE of Jaqué, 29 Apr. 1980, *N. Garwood 972* (holotype, MO-2994466!; isotype, MO-29944671!).

Habitat and distribution. This species is known from lowland wet forest vegetation in eastern Panama and northwestern Colombia (Antioquia, Chocó; Gentry, 1985).

18. Adenocalymma cidii (A. H. Gentry ex Hauk) L. G. Lohmann, comb. nov. Basionym: *Memora cidii* A. H. Gentry ex Hauk, Novon 9: 48, fig. 1. 1999. *Adenocalymma cidii* (A. H. Gentry ex Hauk) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Novo Aripuanã, BR 230, Rod. Transamazônica, 400 km N of Humaitá, 7°15′S, 60°00′W, 4 May 1985, *C. A. Cid Ferreira 6013* (holotype, MO-3506581!; isotypes, F-2047265 image!, NY image!).

Habitat and distribution. This species is known from wet forest vegetation in Amazonian Brazil (Amazonas) and Peru (Loreto).

19. Adenocalymma cladotrichum (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Memora cladotricha* Sandwith, Kew Bull. 8(4): 482. 1953 [1954]. TYPE: Colombia. Meta: Sierra de la Macarena, Río Guapaya, 500 m, 18 Jan. 1950, *W. R. Philipson, J. Idrobo & R. Jaramillo 2123* (holotype, BM!, BM as photo K neg. 856 at K!; isotype, US-2045137 image!).

Habitat and distribution. This species is known from evergreen forest vegetation (Gentry, 1997) in Colombia (Amazonas, Caquetá, Meta, Vaupés), Venezuela (Amazonas, Apure, Barinas, Bolívar, Carabobo, Falcón, Mérida, Miranda, Táchira, Trujillo, Yaracuy, Zulia), Ecuador, Peru (Amazonas, Huánuco, Loreto, San Martín, Ucayali), and Brazil (Acre).

20. Adenocalymma comosum (Cham.) DC., in A. DC., Prodr. 9: 201. 1845. *Bignonia comosa* Cham., Linnaea 7: 693. 1832 [1833]. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18461 at MO-1692901!, K!, K as photo K neg. 11555 at K!, K as photocopy at MO-2692315!, NY-313142!, RB-161655!, RB as photocopy at MO-230038!).

Habitat and distribution. This species is found in Atlantic forest vegetation in Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Pernambuco, Rio de Janeiro, Santa Catarina, São Paulo).

21. Adenocalymma contractum (A. H. Gentry ex Hauk) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Memora contracta* A. H. Gentry ex Hauk, Novon 9(1): 50. 1999. TYPE: Brazil. Rondônia: SW Ariquemes, Mineiração

Mibrasa, Setor Alto Candeias, Km. 128, 10°35′S, 63°35′W, 16 May 1982, *L. O. A. Teixeira, A. J. Fife, K. McFarland, C. D. A. Mota, J. L. dos Santos, S. P. Gomes & B. W. Nelson 502* (holotype, MO-3237252!; isotypes, INPA-104239!, K!, NY-328885!, NY-328886!).

Habitat and distribution. This species is known from wet forest vegetation in Venezuela (Bolívar), Guyana, and Brazil (Amazonas, Pará, Rondônia).

22. Adenocalymma coriaceum A. DC., Prodr. 9: 202. 1845. TYPE: Brazil. Bahia: Bahia meridional, 1840, *J. S. Blanchet 3221* (holotype, G-DC!, G-DC as photo F neg. 7648 at MO-1692802!; isotypes, P [barcode] P00468574! P [barcode] P00468575!, P [barcode] P00468576!, P specimens without barcodes as photocopies at MO-2294486!, MO-2294487!, MO-2294601!).

Habitat and distribution. This species is known from Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo).

23. Adenocalymma cristacalyx (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora cristacalyx* A. H. Gentry, Ann. Missouri Bot. Gard. 64(2): 316. 1977 [1978]. TYPE: Brazil. Ceará: s. loc., *F. F. Allemão & [init. unknown] Cisneiros 1045* (holotype, R-127332 not seen; isotype, MO-2305584!).

Habitat and distribution. This species is found in dry vegetation in northeastern Brazil (Ceará, Paraíba).

24. Adenocalymma croatii (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora croatii* A. H. Gentry, Ann. Missouri Bot. Gard. 61(3): 877. 1974. *Adenocalymma croatii* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Peru. Loreto: 7 km NE of Río Nanay & Puerto Almendra, 23 July 1972, *T. B. Croat 18335* (holotype, MO-2100198!; isotypes, F-1808202 image!, MO-2103338!, PMA not seen, USM not seen, VEN not seen).

Habitat and distribution. This species is known from wet forest vegetation in Colombia (Amazonas), Peru (Amazonas, Ucayali), and Brazil (Acre, Amazonas).

25. Adenocalymma cymbalum (Cham.) Bureau & K. Schum., Fl. Bras. 8(2): 112. 1896. *Bignonia cymbalum* Cham., Linnaea 7: 716. 1832 [1833]. TYPE: Brazil. s. loc, s.d., *F. Sellow 1613* (holotype, LE not seen; isotype, B†, B as photo F neg. 18482 at MO-1692883!).

Habitat and distribution. This species is known from humid forest vegetation in northern Brazil (Maranhão, Pará) and Atlantic forest vegetation in eastern and southeastern Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

26. Adenocalymma dichilum A. H. Gentry, Novon 3(2): 137. 1993. TYPE: Brazil. Piauí: betw. Bom Jesus & São Raimundo Nonato, 11 May 1979, *A. Fernandes s.n.* (holotype, EAC-6185!; isotype, MO-3204496!).

Habitat and distribution. This species is known from dry caatinga vegetation in northeastern and eastern Brazil (Bahia, Ceará, Piauí).

27. Adenocalymma divaricatum Miers, Ann. Mag. Nat. Hist., sér. 3, 7: 390. 1861. TYPE: Brazil. Bahia: Rio de Janeiro, ad montem Corcovado, *J. Miers 3383* (holotype, P [barcode] P00468577 image!).

Habitat and distribution. This species is known from dry caatinga vegetation and deciduous forests in Brazil (Bahia, Espírito Santo, Minas Gerais, Piauí, Rio de Janeiro).

28. Adenocalymma dugandii Sandwith, Kew Bull. 8(4): 479. 1953 [1954]. TYPE: Colombia. Cundinamarca: Hacienda El Cucharo, betw. Tocaima & Pubenza, 350 m, 7 May 1944, *E. P. Killip, A. Dugand & R. Jaramillo 38326* (holotype, K!; isotype, US-1856145 image!).

Habitat and distribution. This species is known from wet forest vegetation in central Colombia (Cundinamarca, Tolima).

29. Adenocalymma dusenii Kraenzl., Repert. Spec. Nov. Regni. Veg. 17: 115. 1921. TYPE: Brazil. Paraná: Itupava, 5 June 1909, *P. Dusén 8215* (holotype, S not seen, S as photocopy at MO-2909905!).

Habitat and distribution. This species is found in forest vegetation in southern Brazil (Paraná, Santa Catarina).

30. Adenocalymma flaviflorum (Miq.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Spathodea flaviflora* Miq., Stirp. Surinam. Select. 124. 1850 [1851]. *Memora flaviflora* (Miq.) Pulle, Enum. Vasc. Pl. Surinam 427. 1906. TYPE: Suriname. s. loc., Aug. 1847,

A. Kappler 1865 (holotype, U not seen; isotype, P [barcode] P00481556!).

Habitat and distribution. This species is widely found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Amazonas, Apure, Bolívar, Táchira), Guyana, Suriname, French Guiana, Peru (Loreto), and Brazil (Amazonas, Maranhão, Pará).

31. Adenocalymma flavum Mart. ex DC., in A. DC., Prodr. 9: 202. 1845. TYPE: Brazil. Bahia; Ilhéus, ad viam Felisberti, 1816, *Prince A. P. M. Wied-Neuwied in herb. Martius s.n.* (lectotype, designated here, BR-880369!; isolectotypes, BR- 880352!, BR-880385!, G-DC!).

Nomenclatural note. Part of Martius's herbarium has been transferred to BR, and therefore this represents original material. There are three duplicates of the type collection there and the best material is selected as the lectotype.

Habitat and distribution. This species is known from wet forest vegetation in eastern Brazil (Bahia, Espírito Santo).

32. Adenocalymma fruticosum A. H. Gentry, Novon 3(2): 137. 1993. TYPE: Brazil. Bahia: Serra do Sincorá, 6 km N of Cascavel on rd. to Mucugê, 1200 m, 13°06′S, 41°25′W, 25 Mar. 1980, *R. M. Harley, G. L. Bromley, A. M. de Carvalho & G. Martinelli 20943* (holotype, CEPEC not seen; isotypes, K!, MO-2918696!).

Habitat and distribution. This species is known from campo geral (i.e., grassland vegetation that is also rich in dicot herbs, shrubs, and acaulous palms) in the Serra do Sincorá in eastern Brazil (Bahia).

33. Adenocalymma gracielzae A. H. Gentry, Novon 3(2): 138. 1993. TYPE: Brazil. Pará: Senador José Porfirio, Rio Xingú, 3 Dec. 1991, *G. dos Santos, N. A. Rosa & M. R. dos Santos 276* (holotype, MG not seen; isotypes, MAD not seen, MO-4089769!).

Habitat and distribution. This species is known from restinga and riverside scrub vegetation along the River Xingú and its tributaries in northeastern Brazil (Pará; Gentry, 1993).

34. Adenocalymma grandifolium Mart. ex DC., in A. DC., Prodr. 9: 199. 1845. *Bignonia grandifolia* Vell., Fl. Flumin. 247. 1825 [1829], Fl. Flum. Icon. 6: tab. 28. 1827 [1831], hom. illeg., non *Bignonia grandifolia* Jacq., 1798. *Adenocalymma prasinum* Miers, Ann. Mag. Nat. Hist., Ser. 3, 7: 395. 1861, nom. superfl. TYPE: tab. 28 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated by Laroche [1973: 6]).

Nomenclatural note. De Candolle's name was based on Vellozo's species *Bignonia grandifolia*, and thus must be typified by Vellozo's materials. However, Vellozo's name was an illegitimate later homonym and thus cannot be a basionym for a nomenclatural combination, so de Candolle's name is effectively a replacement name. Miers's name *Adenocalymma prasinum* was an avowed substitute for *A. grandifolium*, but it was not needed because de Candolle's earlier name was available and thus is superfluous.

Habitat and distribution. This species is found in wet vegetation in southeastern Brazil (Rio de Janeiro).

35. Adenocalymma hatschbachii A. H. Gentry, Novon 3(2): 139. 1993. TYPE: Brazil. Paraná: Morro do Arrastão, Mun. Morretes, 200 m, 18 July 1981, *G. Hatschbach 43956* (holotype, MO-2925256!; isotype, MBM not seen).

Habitat and distribution. This species is known from wet subtropical forest vegetation in southeastern Brazil, near sea level from Paraná to southern São Paulo State and to higher elevations in Rio de Janeiro State (Gentry, 1993).

36. Adenocalymma heterophyllum Kraenzl., Notizbl. Königl. Bot. Gart. Berlin 6: 372. 1915. *Memora heterophylla* (Kraenzl.) Sandwith, Receuil Trav. Bot. Néerl. 34: 214. 1937. TYPE: Brazil. Acre: Rio Branco, Jan. 1909, *E. Ule 7849* (holotype, B†; lectotype, designated here, K [barcode] K000449764!; isolectotype, MG-12942 not seen, MG-12942 as photocopy at MO-2300101!).

Habitat and distribution. This species is known from riparian lowland vegetation (Gentry, 1997) in Venezuela (Amazonas), Guyana, and Brazil (Amazonas, Pará, Roraima).

37. Adenocalymma hirtum (Mart. ex DC.) Bureau & K. Schum., Fl. Bras. 8(2): 100. 1896. *Tecoma hirta* Mart. ex DC., in A. DC., Prodr. 9: 222. 1845. TYPE: Brazil. Rio de Janeiro, Dec., *C. F. P. von Martius s.n.* (holotype, M-86330!, M as photo F neg. 20447 at MO-1692808!; isotype, G-DC!).

Habitat and distribution. This species is known from Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, São Paulo).

38. Adenocalymma hypostictum Bureau & K. Schum., Fl. Bras. 8(2): 99. 1896. TYPE: Brazil. Minas Gerais: s. loc., s.d., *A. Glaziou 15257* (holotype, P not seen, P as photocopy at MO-2294482!; isotype, B†, B as photo F neg. 18464 at MO-1692809!).

Habitat and distribution. This species is known from Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Pernambuco, Rio de Janeiro).

39. Adenocalymma imperatoris-maximilianii (Wawra) L. G. Lohmann, comb. nov. Basionym: *Bignonia imperatoris-maximilianii* Wawra, Bot. Ergebn. 73, tab. 10. 1866. *Pleonotoma imperatoris-maximilianii* (Wawra) Bureau & K. Schum., Fl. Bras. 8(2): 279. 1896 [1897]. *Memora imperatoris-maximilianii* (Wawra) A. H. Gentry, Ann. Missouri Bot. Gard. 64(2): 316. 1977 [1978]. *Adenocalymma imperatoris-maximilianii* (Wawra) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Itapema, s.d., *H. Wawra & F. Maly 156* (holotype, W!, W as photo F neg. 32874 at MO-1693043!).

Habitat and distribution. This species is known from seasonal vegetation in northeastern and eastern Brazil (Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí).

40. Adenocalymma impressum (Rusby) Sandwith, Recueil Trav. Bot. Néerl. 34: 212. 1937. *Bignonia impressa* Rusby, Mem. Torrey Bot. Club 6: 100. 1896 [1897]. TYPE: Bolivia. La Paz: Guanai-Tipuni, Apr.–June 1892, *A. M. Bang 1321* (lectotype, designated here, NY-579086!; isolectotypes, F-160450 image!, G-8979!, G-14106!, G-14107!, K!, M-86329!, MO-2005552!, NY-579085!, US-47712 image!, US-1322433 image!).

Nomenclatural note. Two duplicates of the type collection were located at NY. One has the original handwritten label and a well-preserved flower, while the other has a printed label as well as part of a page from the publication of this species name mounted on it and was previously deposited in the Columbia College herbarium where Rusby worked. The specimen with the handwritten label and better flowers is chosen as the lectotype.

Habitat and distribution. This species is known from humid to dry lowland forest vegetation in Colombia (Amazonas), Venezuela (Amazonas, Apure, Bolívar), French Guiana, Ecuador, Peru (Huánuco, Loreto, Madre de Dios, Pasco, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Pará).

41. Adenocalymma inundatum Mart. ex DC., in A. DC., Prodr. 9: 201. 1845. TYPE: Brazil. Pará: island of Marajó, Aug. 1819, *C. F. P. von Martius s.n.* (lectotype, designated here, M-86326!, M as photo F neg. 20448 at MO-1692810!; isolectotypes, M-86327!, M-86328!).

Nomenclatural note. Three duplicates of this type were deposited at M and the single flowering specimen is here selected as the lectotype.

Habitat and distribution. This species is found in humid lowland forest vegetation in Mexico (Campeche, Chiapas, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, Puebla, Sinaloa, Tabasco, Veracruz), the Lesser Antilles (Grenada, St. Lucia, St. Vincent), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Magdalena, Santander, Sucre), Venezuela (Bolívar, Lara, Nueva Esparta, Sucre, Táchira, Trujillo, Zulia), Guyana, French Guiana, Ecuador, Peru (Loreto, Madre de Dios), and Brazil (Amapá, Amazonas, Maranhão, Pará, Roraima).

42. Adenocalymma involucratum (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Memora involucrata* Bureau & K. Schum., Fl. Bras. 8(2): 271. 1896 [1897]. *Pharseophora involucrata* Miers, Proc. Roy. Hort. Soc. London 3: 186. 1863, nom. nud. *Adenocalymma involucratum* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Piauí: Oieiras, Mar. 1839, *G. Gardner 2241* (holotype, P [barcode] P00481552!; isotypes, BM-571229!, F-1012428 image!, K!, NY-328898!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Goiás, Maranhão, Minas Gerais, Piauí, Tocantins).

43. Adenocalymma juliae (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora juliae* A. H. Gentry, Ann. Missouri Bot. Gard. 68(1): 118. 1981. *Adenocalymma juliae* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Peru. Loreto: Maynas, Río Yaguasyacu, tributary of Río Amapiyacu, below Borro Indian village of Villa Nueva, 7 Nov. 1977, *A. H. Gentry & J. Revilla 20348* (holotype, MO-2658634!; isotypes,

AMAZ not seen, F-1844726 image!, GH not seen, NY-73993!, USM not seen).

Habitat and distribution. This species is found in seasonally flooded forest vegetation in Amazonian Peru (Loreto) and Brazil (Amazonas, Pará).

44. Adenocalymma longilineum (A. Samp.) L. G. Lohmann, comb. nov. Basionym: *Memora longilinea* A. Samp., Bol. Mus. Nac. Rio de Janeiro 12(3, 4): 85. 1936. *Adenocalymma longilineum* (A. Samp.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus, estrada do Aleixo, 14 June 1933, *A. Ducke 1934* (holotype, RB-24097 [barcode] RB00659635!; isotypes, RB-24097 [barcode] RB00536903!, RB-24097 [barcode] RB00659596!, K!).

Habitat and distribution. This species is found in wet lowland forest vegetation in Amazonian Bolivia and Brazil (Acre, Amazonas, Pará, Rondônia).

45. Adenocalymma magdalenense Dugand, Caldasia 4: 61. 1946. TYPE: Colombia. Magdalena: Aracataca, hacienda Macaraquilla, 30 m, 20 Jan. 1940, *A. Dugand & H. Garcia-Barriga 2480* (holotype, COL-23167 not seen).

Habitat and distribution. This species is found in wet lowland forest vegetation in the lower Magdalena River valley in northern Colombia (Bolívar, Magdalena).

46. Adenocalymma magnificum Mart. ex DC., in A. DC., Prodr. 9: 202. 1845. *Memora magnifica* (Mart. ex DC.) Bureau, in Warm., Kongel. Danske Vidensk. Selsk. Skr., Naturvifrsnk. Math. Afh. 1893: 106. 1893 [1894]. TYPE: Brazil. Pará: near Canumã & Rio Amazonas, Apr. 1820, *C. F. P. von Martius 2592* (lectotype, designated here, M-86283!, M as photo F neg. 20487 at MO-1693008!, M as photo K neg. 5941 at K!; isolectotypes, K!, M-86282!, M-86262 as photo K neg. 5939 at K!, M-86284!, M-86284 as photo K neg. 5940 at K!, M-86285!, M-86286!, M-86286 as photo K neg. 5943 at K!, M-86287!).

Nomenclatural note. Original material of this species appears to be at M, and the best sheet deposited there is selected as the lectotype.

Habitat and distribution. This species is found in wet lowland forest vegetation in Amazonian Brazil (Amazonas, Maranhão, Pará, Roraima).

47. Adenocalymma magnoalatum Scud., Novon 10(3): 234, fig. 1. 2000. TYPE: Brazil. Minas Gerais: Marliéria, Parque Estadual do Rio Doce, 10 Oct. 1996, *V. V. Scudeller 579* (holotype, VIC!; isotype, MO not seen).

Habitat and distribution. This species is known from only a few collections in Atlantic forest vegetation in eastern Brazil (Minas Gerais).

48. Adenocalymma marginatum (Cham.) DC., in A. DC., Prodr. 9: 200. 1845. *Bignonia marginata* Cham., Linnaea 7: 695. 1832 [1833]. TYPE: Brazil. Santa Catarina: s. loc., s.d., *F. Sellow 5581* (holotype, LE not seen).

Nomenclatural note. Sandwith and Hunt (1974) discussed the typification of this name and concluded that the protologue cited two specimens: a Chamisso collection from Fretum Sanctae Catharinae, today's Florianópolis, and a Sellow collection from Misitque. However, Chamisso did not visit Brazil, and the full information given in the protologue about the Sellow collection was Misitque e Brasilia Sellowius, which means sent from Brazil by Sellow. Thus only one Sellow collection was cited for this species, which is here considered the type. A photo of a Sellow specimen deposited at B was distributed as a photo of the type of this name (photo F neg. 18465 at MO-1692814!), but this specimen has since been destroyed. The specimen in the photo has the name *Bignonia marginata* and an identification of Sellow as the collector in one handwriting on one label, with no collection number noted here, and an annotation of the number 5581 and the locality São Paulo written in another handwriting on an additional label that is glued onto the first label. Thus this specimen does not appear to have been a type.

Habitat and distribution. This species is found in dry forest vegetation in Paraguay, Brazil (Alagoas, Bahia, Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo), Uruguay, and Argentina (Corrientes, Entre Ríos, Misiones).

49. Adenocalymma molle (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora mollis* A. H. Gentry, Phytologia 46(4): 211. 1980. *Adenocalymma molle* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus–Caracaraí Hwy., 3 km W of Reserva Experimental Station of INPA, Km. 60, 15 Aug. 1974, *G. T. Prance, T. D. Pennington, B. W. Nelson & J. F. Ramos 21658* (holotype, INPA

not seen; isotypes, MG not seen, MO-2236218!, NY-232334!).

Habitat and distribution. This species is known from wet lowland forest vegetation in Amazonian Brazil (Amazonas, Pará).

50. Adenocalymma moringifolium (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia moringifolia* DC., in A. DC., Prodr. 9: 170. 1845, as "moringaefolia." *Pleonotoma moringifolia* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 184. 1863. *Memora moringifolia* (DC.) Sandwith, Receuil Trav. Bot. Néerl. 34: 207. 1937. *Adenocalymma moringifolium* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 759. 2010, nom. nud. invalid. TYPE: French Guiana. Cayenne, s.d., *Anonymous s.n.* (holotype, P [barcode] P00410843!, P as photocopy at MO-2904517!, P as photo F neg. 39935 at K!).

Habitat and distribution. This species is found in wet forest vegetation in Suriname, French Guiana, and Brazil (Amazonas, Pará).

51. Adenocalymma nervosum Bureau & K. Schum., Fl. Bras. 8(2): 95. 1896. TYPE: Brazil. Minas Gerais: s. loc., s.d., *G. Schüch s.n.* (lectotype, designated here, W!, W as photo F neg. 32841 at K!, W as photo F neg. 32841 at MO-1692823!; isolectotype, P, not seen, P as photocopy at MO-2927301!).

Nomenclatural note. Two syntypes from Minas Gerais, *Schüch s.n.* and *Ackermann s.n.*, were cited in the protologue. The Schüch collection was seen in W, and the Ackermann collection in BR. The Schüch collection is more complete and in better condition, and photographs of this but not the Ackermann collection were distributed in the F negative series and are widely available. Therefore, the Schüch collection at W is here designated as the lectotype.

Habitat and distribution. This species is known only from forest vegetation in southeastern Brazil (Minas Gerais).

52. Adenocalymma nodosum (Silva Manso) L. G. Lohmann, comb. nov. Basionym: *Bignonia nodosa* Silva Manso, Enum. Subst. Braz. 40. 1836. *Memora nodosa* (Silva Manso) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. *Adenocalymma nodosum* (Silva Manso) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Cuiabá, s. loc., s.d., *A. Silva Manso s.n.* (holotype, not located).

Nomenclatural note. Type materials have not been located so far, so further studies are necessary to clarify the typification of this species.

Habitat and distribution. This species is known from cerrado vegetation in central and southeastern Brazil (Goiás, Mato Grosso, Minas Gerais, Piauí, Rio de Janeiro, Tocantins).

53. Adenocalymma patulum (Miers) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Memora patula* Miers, Proc. Roy. Hort. Soc. London 4: 161. 1864. TYPE: Colombia. Magdalena: Río Magdalena, July 1868, *M. Weir 35* (holotype, K!).

Habitat and distribution. This species is known from semideciduous lowland forest vegetation (Gentry, 1997) in Colombia (Antioquia, Atlántico, Bolívar, Cundinamarca, La Guajira, Magdalena, Sucre), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Bolívar, Carabobo, Cojedes, Falcón, Guárico, Lara, Miranda, Monagas, Sucre, Zulia), and possibly Peru (San Martín).

54. Adenocalymma paucifoliolatum (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora paucifoliolata* A. H. Gentry, Ann. Missouri Bot. Gard. 61(3): 878. 1974. *Adenocalymma paucifoliolatum* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: Brazil. Goiás: 10 km W of Cristalina, 1200 m, 4 Mar. 1966, *H. S. Irwin, J. R. Grear, Jr., R. Souza & R. Reis dos Santos 13438* (holotype, UB not seen; isotypes, K!, MO-2092446!).

Habitat and distribution. This species is found in cerrado vegetation in central to southeastern Brazil (Bahia, Goiás, Minas Gerais, Tocantins, Pará).

55. Adenocalymma paulistarum Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. TYPE: Brazil. São Paulo: prope Campinas, *J. Correia de Méllo 28* (lectotype, designated here, S04-3475 image!; isolectotypes, K [barcode] K000449348 image!, K [barcode] K000449349 image!, US-01706100 image!).

Nomenclatural note. No specimens were cited in the protologue of this species, which was very synoptic, but three specimens were cited by Bureau and Schumann (1896). These were a Sellow specimen without collection number or locality data; the collection *A. F. Regnell III-902*, from Caldas in Minas Gerais; and the collection *Correia de Méllo 28* from Campinas in São Paulo. Any duplicates of these

specimens that were deposited at B are now lost. Sellow material corresponding to this species has not been located. There is a duplicate of the Regnell collection at BR (BR-880349!), which has only a few flowers that have been damaged by insects. There are several duplicates of the Correia de Méllo collection that have good flowers in good condition, and this is chosen here as the type. No duplicates of this collection were found at P, but there are two specimens at K, one with a small inflorescence with an immature fruit and several young flower buds, and a second one with a sterile branch and three loose flowers in the packet, as well as specimens at S and US that have good leaves and a fully developed inflorescence with multiple mature flowers. The exemplary specimen at S is here chosen as the lectotype.

Habitat and distribution. This species is only known from wet forest vegetation in southeastern Brazil (São Paulo) and Argentina (Misiones).

56. Adenocalymma pedunculatum (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia pedunculata* Vell., Fl. Flumin. 250. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 41. 1827 [1831]. *Memora pedunculata* (Vell.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. *Adenocalymma pedunculatum* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: tab. 41 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in forest and cerrado vegetation in Brazil (Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, São Paulo, Tocantins).

57. Adenocalymma peregrinum (Miers) L. G. Lohmann, comb. nov. Basionym: *Pleonotoma peregrina* Miers, Proc. Roy. Hort. Soc. London 3: 183. 1863. *Memora peregrina* (Miers) Sandwith, Kew Bull. 8(4): 483. 1953 [1954]. *Adenocalymma peregrinum* (Miers) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1582. 2008, nom. nud. invalid. *Adenocalymma peregrinum* (Miers) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: Brazil. São Paulo: s. loc., 1861–1862, *M. Weir 152* (holotype, K!; isotype, BM!).

Habitat and distribution. This species is found in cerrado vegetation in Brazil (Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, São Paulo) and Paraguay.

58. Adenocalymma prancei A. H. Gentry, Ann. Missouri Bot. Gard. 65(2): 725. 1978 [1979]. TYPE: Brazil. Amazonas: 3–6 km N of Manaus–Itacoatiara Rd., near Rio Preto da Eva (Km. 79), 3 Dec. 1974, *A. H. Gentry & J. Ramos 13063* (holotype, INPA not seen; isotypes, MG not seen, MO-2257039!).

Habitat and distribution. This species is found in wet lowland forest vegetation in French Guiana and Amazonian Brazil (Amazonas, Pará).

59. Adenocalymma pseudopatulum (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 280. 2008. *Memora pseudopatula* A. H. Gentry, Ann. Missouri Bot. Gard. 68(1): 119. 1981. TYPE: Peru. Loreto: Río Mazán, just above La Libertad, ca. 35 km above Mazán, ca. 150 m, 10 July 1976, *A. H. Gentry & J. Revilla 16617* (holotype, MO-2690665!; isotypes, AMAZ not seen, COL not seen, F-1855573 image!, INPA not seen, MO-2690654!, US-2892289 image!, USM not seen).

Habitat and distribution. This species is found in seasonally flooded forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Amazonas), Peru (Amazonas), and Brazil (Acre).

60. Adenocalymma pubescens (Spreng.) L. G. Lohmann, comb. nov. Basionym: *Amphilophium pubescens* Spreng., Syst. Veg. 2: 836. 1825. *Bignonia fallax* Cham., Linnaea 7: 717. 1832 [1833], replacement name, non *Bignonia pubescens* L., 1763. *Pharseophora fallax* (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863, nom. illeg. *Memora fallax* (Cham.) Bureau, in Warm., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afh. 1893: 105 1893, nom. illeg. *Memora pubescens* (Spreng.) K. Schum., Nat. Pflanzenfam. 4(3b): 226. 1894. *Macfadyena fallax* (Cham.) S. Moore, Trans. Linn. Soc. London, Bot. 4: 418. 1895, non *Macfadyena pubescens* S. Moore, 1895. *Adenocalymma pubescens* (Spreng.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: Brazil. S. loc., s.d., *F. Sellow s.n.* (holotype, B†; lectotype, designated here, K!).

Nomenclatural note. Miers's name *Pharseophora fallax* is illegitimate because the earlier epithet "pubescens" was available in *Pharseophora*, and correctly should have been used. The name *Memora fallax* is similarly illegitimate because the epithet "pubescens" was available in *Memora* and correctly should have been used instead of "fallax." However,

the name *Macfadyena fallax* is legitimate because the epithet pubescens was previously used in that genus for a different species and thus was not available for this species. Only one isotype was found and is designated as the lectotype here.

Habitat and distribution. This species is found in dry vegetation in central Brazil (Ceará, Goiás, Maranhão, Pernambuco, Piauí, Tocantins) and Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Minas Gerais, São Paulo).

61. Adenocalymma purpurascens Rusby, Descr. S. Amer. Pl. 121. 1920. TYPE: Venezuela. Lower Orinoco, 1896, *H. H. Rusby & R. W. Squires s.n.* (holotype, NY-313044!, NY as photo K neg. 3388 at K!).

Habitat and distribution. This species is widespread in evergreen forest vegetation (Gentry, 1997) in Colombia (Amazonas, Meta), Venezuela (Amazonas, Bolívar, Delta Amacuro), Guyana, Suriname, French Guiana, Ecuador, Peru (Huáncuo, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín), Bolivia, and Brazil (Amazonas, Maranhão, Mato Grosso, Pará, Rôndonia).

62. Adenocalymma racemosum (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Memora racemosa* A. H. Gentry, Ann. Missouri Bot. Gard. 65(2): 731. 1978 [1979]. *Adenocalymma racemosum* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 760. 2010, nom. nud. invalid. TYPE: Brazil. Pará: Km. 93 of Belém–Brasília Hwy., 5 Aug. 1963, *B. Maguire, J. Murça Pires, C. K. Maguire & N. T. Silva 56008* (holotype, MO-2232814!; isotypes, COL-114245 image!, F-1812279 image!, MO-2279292!, NY [barcode] NY00328889!, NY [barcode] NY00328890!).

Habitat and distribution. This species is found in wet forest vegetation in Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Maranhão, Mato Grosso, Pará).

63. Adenocalymma reticulatum Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. TYPE: Brazil. Minas Gerais: s. loc., s.d., *C. F. P. von Martius s.n.* (holotype, BR-880382!, BR as photo K neg. 2046 at K!, BR as photo K neg. 2046 at MO-3694056!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Bahia, Minas Gerais, Rio de Janeiro).

64. Adenocalymma salmoneum J. C. Gomes, Dusenia 2: 314, tab. 4, figs. 1–6. 1951. TYPE: Brazil. Espírito Santo: N of Rio Doce, margin of River São Gabriel, Sep. 1950, *J. N. Vieira 20* (holotype, RB-71152!; isotype, MBML not seen).

Habitat and distribution. This species is restricted to wet forest vegetation in eastern Brazil (Espírito Santo, Minas Gerais).

65. Adenocalymma salzmanii DC., in A. DC., Prodr. 9: 200. 1845. TYPE: Brazil. Bahia: s. loc., s.d., *P. Salzmann 341* (holotype, G-DC not seen, G-DC as photo F neg. 7647 at MO-1692816!).

Habitat and distribution. This species is restricted to dry forest vegetation in eastern Brazil (Bahia).

66. Adenocalymma sastrei (A. H. Gentry ex Hauk) L. G. Lohmann, comb. nov. Basionym: *Memora sastrei* A. H. Gentry ex Hauk, Novon 9(1): 52. 1999. Colombia. Amazonas: Río Igará-Paraná, La Chorrera, 22 Sep. 1973, *C. Sastre 2293* (holotype, MO-2637040!; isotype, P!, P as photocopy at MO-05060095!).

Habitat and distribution. This species is known only from the type locality in southern Colombia (Amazonas).

67. Adenocalymma saulense A. H. Gentry, Novon 3(2): 140. 1993. TYPE: French Guiana. Saül: La Fume Mountain Trail, 3°37′N, 53°12′W, 250–350 m, 27 Aug. 1988, *S. A. Mori, C. Gracie, L. Flynn, W. Pagels, C. James, W. Capraro, L. Connick, P. O'Malley, D. Vuillequez & H. Betros 19192* (holotype, MO-3600685!; isotypes, CAY!, NY [barcode] NY00039315!).

Habitat and distribution. This species is known only from the Saül area of southern French Guiana, where it occurs in well-drained, moist forests on lateritic soils (Gentry, 1993).

68. Adenocalymma scabriusculum Mart. ex DC., in A. DC., Prodr. 9: 201. 1845. TYPE: Brazil. Piauí: betw. Oeiras & Olho D'água, May 1817, *C. F. P. von Martius 2900* (lectotype, designated here, M-86322!, M as photo F neg. 20451 at MO-1692817!, M as photo K neg. 5956 at K!; isolectotype, M-86323!, M as photo K neg. 5955 at K!).

Nomenclatural note. Original type material of this name is at M. Two duplicates are deposited there and the best material is selected here as the lectotype.

Habitat and distribution. This species is found in dry caatinga vegetation in central Brazil (Goiás, Maranhão, Piauí, Tocantins).

69. Adenocalymma scansile Miers, Ann. Mag. Nat. Hist., ser. 3, 7: 388. 1861. TYPE: Brazil. Rio de Janeiro (not located).

Nomenclatural note. The type of this name was not detailed in the protologue and has not yet been identified or located. More study is needed before its typification can be clarified.

Habitat and distribution. This species is found in tropical and subtropical forest vegetation in Paraguay, Brazil (Minas Gerais, Paraná, Rio de Janeiro, São Paulo, Santa Catarina), and Argentina (Misiones).

70. Adenocalymma schomburgkii (DC.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Spathodea schomburgkii* DC., in A. DC., Prodr. 9: 207. 1845. *Memora schomburgkii* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. TYPE: British Guiana [Guyana]. s. loc., 1837, *Rob. Schomburgk ser. I, 365* (holotype, G-DC!, G-DC as photo F neg. 7693 at MO-1693061!; isotypes, BM!, K!).

Habitat and distribution. This species is found in seasonally inundated lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Caquetá, Guainía, Vaupes), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Ecuador, Peru (Loreto), and Brazil (Acre, Amapá, Amazonas, Maranhão, Pará, Rôndonia, Roraima).

71. Adenocalymma sousae A. H. Gentry, Fl. Veracruz 24: 22. 1982. TYPE: Mexico. Veracruz: Río Chuniapa, Sontecomapa, Los Tuxtlas, 26 Aug. 1974, *M. Sousa 4430* (holotype, MEXU not seen, MEXU as photocopy at MO-2900637!).

Habitat and distribution. This species is found in coastal mangroves along the southernmost Gulf of Mexico (Tabasco, Veracruz; Gentry, 1982).

72. Adenocalymma subincanum Huber, Bull. Soc. Bot. Genève, sér 2, 6: 201. 1914 [1915]. TYPE: Brazil. Pará: Almeirino, Pedreira do Rio Arrayollos, 26 Apr. 1903, *A. Ducke 3524* (holotype, MG not seen; isotype, RB-22708!, RB-22708 as photocopy at MO-2692483!).

Habitat and distribution. This species is found in wet forests in French Guiana and the northeastern to western Amazon basin of Brazil (Acre, Amazonas, Maranhão, Pará) and perhaps Peru (Huánuco).

73. Adenocalymma subsessilifolium DC., in A. DC., Prodr. 9: 199. 1845. TYPE: Brazil. Rio de Janeiro, 1832, *J. Lhotsky s.n.* (holotype, G-DC!, G-DC as photo F neg. 7649 at MO-1692819!).

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

74. Adenocalymma subspicatum A. H. Gentry, Novon 3(2): 140. 1993. TYPE: Brazil. Ceará: sítio Pará, Viçosa do Ceará, 12 June 1979, *A. Fernandes, P. Martins & F. Matos s.n.* (holotype, EAC-6501 not seen; isotype, MO-3204488!).

Habitat and distribution. This species is found in dry carrasco and caatinga vegetation in northeastern Brazil (Ceará, Maranhão, Piauí).

75. Adenocalymma tanaeciicarpum (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Memora tanaeciicarpa* A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 57. 1976. TYPE: Brazil. Amazonas: s. loc., 16 May 1972, *A. Loureiro, O. Pires & [initial unknown] Athengildo INPA-35794* (holotype, MO-2228097!; isotype, INPA-35794!).

Habitat and distribution. This species is found in flooded lowland riverside forest vegetation (Gentry, 1997) in Colombia (Vaupés), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, and Brazil (Amazonas, Pará).

76. Adenocalymma ternatum (Vell.) Corr. Méllo ex Bureau & K. Schum., Fl. Bras. 8(2): 104. 1896. *Bignonia ternata* Vell., Fl. Flumin. 246. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 21. 1827 [1831]. TYPE: tab. 21 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern and southeastern Brazil (Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Rio de Janeiro).

77. Adenocalymma trichocladum (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia trichoclada* DC., in A. DC., Prodr. 9: 158. 1845. *Arrabidaea trichoclada* (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 49. 1896. *Sampaiella trichoclada* (DC.) J. C. Gomes, Rodriguésia 12(23): 108. 1949. *Adenocalymma trichocladum* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1:

760. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: s. loc., capões & caatingas, 1818, *C. F. P. von Martius s.n.* (holotype, G-DC!; isotype, M not seen, M as F neg. 20444 at MO-1692862!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern and southeastern Brazil (Bahia, Minas Gerais, Piauí, São Paulo).

78. Adenocalymma trifoliatum (Vell.) R. C. Laroche, Loefgrenia 56: 5. 1973. *Bignonia trifoliata* Vell., Fl. Flumin. 245. 1825 [1829]; Fl. Flumin. Icon. 6 tab. 16. 1827 [1831]. TYPE: tab. 16 in Vellozo, Fl. Flumin. Icones 6, 1827 [1831] (lectotype, designated by Laroche [1973: 5]).

Habitat and distribution. This species is found in Atlantic forest vegetation in Brazil (Bahia, Goiás, Minas Gerais, Rio de Janeiro, São Paulo).

79. Adenocalymma ubatubense Assis & Semir, Novon 9(2): 136, fig. 1. 1999, as "*ubatubensis*." TYPE: Brazil. São Paulo: Ubatuba, Picinguaba, 9 May 1990, *R. Romero et al. 74* [sic. in sched., other collectors not named] (holotype, HRCB not seen; isotype, MO-04957521!).

Habitat and distribution. This species is known only from Atlantic forest vegetation in the Ubatuba region in southeastern Brazil (São Paulo).

80. Adenocalymma uleanum Kraenzl., Notizbl. Königl. Bot. Gart. Berlin 6: 372. 1915. TYPE: Peru. Loreto: Yurimaguas, Aug. 1902, *E. Ule 6280* (lectotype, designated here, MG-6151 not seen, MG-6151 as photo K neg. 5472 at K!).

Nomenclatural note. Two syntypes were cited in the protologue, *Ule 6280* and *Ule 9784*, the latter from Seringal Auristella, Alto Acre, Brazil. Only one syntype has been located, and it is here designated as the lectotype.

Habitat and distribution. This species is found in wet lowland forest vegetation in Peru (Huánuco, Loreto, Madre de Dios, Pasco, Puno), Bolivia, and Brazil (Rondônia).

81. Adenocalymma validum (K. Schum.). L. G. Lohmann, comb. nov. Basionym: *Memora valida* K. Schum., Nat. Pflanzenfam. 4(3b): 225. 1894. TYPE: Brazil, s. loc., s.d., *F. Sellow 591* (syntype, B†, B as photo as F neg. 18444 at MO-1693009!), *L. Riedel 756* (syntype, LE not seen, LE as photocopy at MO-297030!).

Bignonia flavida DC., in A. DC., Prodr. 9: 168. 1845, non *Adenocalymma flavidum* Miers, 1861. *Pleonotoma flavida* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. *Memora flavida* (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 264. 1896 [1897]. *Adenocalymma flavidum* (DC.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008, hom. illeg., non *Adenocalymma flavidum* Miers, 1861. *Adenocalymma neoflavida* L. G. Lohmann, Cat. Pl. Fung. Brasil. 1: 769, 2010, nom. nud. invalid. TYPE: Brazil. Pará: Paracajo, Nov. 1819, *C. F. P. von Martius s.n.* (lectotype, designated here, M-86274!, M as photo F neg. 20484 at MO-1693003!; isolectotypes, M-86275!, M-86276!, M-86277!).

Nomenclatural note. The name *Bignonia flavida* is the oldest name for this species, but the epithet "flavidum" has already been used in *Adenocalymma* for another species, *A. flavidum* Miers, and thus cannot be the name for this species. The name *Memora valida* also applies to this species and is therefore here transferred to *Adenocalymma* as the name for this species. The unpublished name that was previously proposed as a replacement name for this species, "A. neoflavidum," is not needed and therefore should not be published, and would be illegitimate if it were published. The type of *M. valida* was not noted in the protologue, which was very synoptic. In their contemporaneous and more detailed treatment, Bureau and Schumann (1896: 264) cited two specimens that are here assumed to comprise the original material on which the description of this species is based. The information available about these materials is currently inadequate to further clarify the typification of *M. valida*. On the other hand, original material of *B. flavida* is deposited at M, where there are four duplicates of the type. The best material is here chosen as the lectotype.

Habitat and distribution. This species is widely distributed in wet and humid forest vegetation in Colombia (Amazonas), Guyana, Suriname, French Guiana, and Brazil (Amazonas, Bahia, Espírito Santo, Pará).

82. Adenocalymma velutinum (A. H. Gentry ex Hauk) L. G. Lohmann, comb. nov. Basionym: *Memora velutina* A. H. Gentry ex Hauk, Novon 9(1): 52, fig. 3. 1999. *Adenocalymma velutinum* (A. H. Gentry ex Hauk) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 770. 2010, nom. nud. invalid. TYPE: Brazil. Pará: BR-230, 188 km W of Altamira, 30 Nov. 1977, *G. T. Prance, A. S. Silva, M. J. Balick, A. J. Henderson, B. W. Nelson & R. P. Bahia 25891* (holotype, INPA not seen; isotypes, MO-2627549!, NY [barcode] NY00073992!, US not seen).

Habitat and distribution. This species is known only from the type collection, from lowland wet forest vegetation in northeastern Brazil (Pará).

II. Amphilophium Kunth, J. Phys. Chim. Hist. Nat. Arts 87: 451. 1818, emend. L. G. Lohmann. TYPE: *Amphilophium paniculatum* (L.) Kunth (lecotype, designated by Fabris [1964: 456]).

Haplolophium Cham., Linnaea 7: 556. 1832 [1833], as "*Aplolophium*," syn. nov. TYPE: *Haplolophium bracteatum* Cham. [≡ *Amphilophium bracteatum* (Cham.) L. G. Lohmann].

Endoloma Raf., Sylva Tellur. 79. 1838. TYPE: *Endoloma purpurea* Raf., nom. illeg. superfl. [≡ *Amphilophium paniculatum* (L.) Kunth].

Distictis Mart. ex Meisn., Pl. Vasc. Gen. 1: 300, 2: 280. 1840, syn. nov. TYPE: *Distictis lactiflora* (Vahl) DC. (lectotype, designated by Sandwith [1962: 454]) [≡ *Amphilophium lactiflorum* (Vahl) L. G. Lohmann].

Pithecoctenium Mart. ex DC., in Meisn., Pl. Vasc. Gen. 1: 300, 2: 208. 1840, syn. nov. *Pithecoxanium*, orth. var. TYPE: *Pithecoctenium echinatum* (Jacq.) Baill. (lectotype, designated by Sandwith [1962: 454]) [= *Amphilophium crucigerum* (L.) L. G. Lohmann].

Phaedranthus Miers, Proc. Roy. Hort. Soc. London 3: 182. 1863. nom. cons., vs. *Sererea* Raf. TYPE: *Phaedranthus lindleyanus* Miers [= *Amphilophium buccinatorium* (DC.) L. G. Lohmann].

Macrodiscus Bureau, Monogr. Bignon. 46, tab. 11. 1864. TYPE: *Macrodiscus rigescens* (Jacq.) Bureau [= *Amphilophium lactiflorum* (Vahl) L. G. Lohmann].

Glaziova Bureau, Adansonia 8: 380. 1868, syn. nov., *Glaziovia*, orth. var. TYPE: *Glaziova bauhinioides* Bureau ex Baill. [≡ *Amphilophium bauhinioides* (Bureau ex Baill.) L. G. Lohmann].

Neves-armondia K. Schum., Nat. Pflanzenfam. Nachtrage Teil 2–4(1): 301, 302. 1897. TYPE: *Neves-armondia cordifolia* (Mart.) K. Schum. [= *Amphilophium falcatum* (Vell.) L. G. Lohmann].

Distictella Kuntze, Lex. Gen. Pl. 182. 1904 [1903], syn. nov. TYPE: *Distictella mansoana* (DC.) Urb. (lectotype, designated by Sandwith [1965: 412]) [≡ *Amphilophium mansoanum* (DC.) L. G. Lohmann].

Wunschmannia Urb., Symb. Antill. 5: 494. 1908. TYPE: *Wunschmannia staminea* (Lam.) Urb. [≡ *Amphilophium stamineum* (Lam.) L. G. Lohmann].

Urbanolophium Melch., Feddes Repert. Beih. 46: 79. 1927, syn. nov. TYPE: *Urbanolophium glaziovii* (Bureau ex K. Schum.) Melch. [= *Amphilophium dusenianum* (Kraenzl.) L. G. Lohmann].

Anomoctenium Pichon, Bull. Soc. Bot. France 92: 226. 1946. TYPE: *Anomoctenium stipulare* (Mart. ex DC.) Pichon [= *Amphilophium frutescens* (DC.) L. G. Lohmann].

Bothriopodium Rizzini, Arch. Jard. Bot. Rio de Janeiro 9: 70. 1949. TYPE: *Bothriopodium glaziovii* (Bureau ex K. Schum.) Rizzini [= *Amphilophium dusenianum* (Kraenzl.) L. G. Lohmann].

Lianas (shrubs), with (without) dimorphic juvenile growth, without strong odor; stems with phloem wedges in multiples of 4 in cross-section, pith solid; branchlets sharply hexagonal or cylindrical, pubescent, without lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds elliptic and foliaceous, with glands. Leaves (1-)2- or 3-foliolate, terminal leaflet often replaced by a trifid (multifid) tendril, tendrils with adhesive disks, without uncinate apices; leaflets coriaceous (membranaceous), with glands sparsely distributed over blade or grouped in vein axils, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a thyrse or raceme. Flowers zygomorphic, pentamerous; calyx cupular, truncate or shortly 5-lobed and frequently with double calyx, coriaceous (membranaceous), puberulous or villose externally, with clusters of glands near margins; corolla white or yellow (magenta, pink, red), without nectar guides, tubular or infundibuliform, straight in tube or bent at ca 90° above base, coriaceous, puberulous to villose (glabrous or lepidote) externally, with glands in lines near margins, lobes 5, imbricate; stamens 4, with well-developed filaments, included (exserted), anthers glabrous, thecae straight, pollen in monads, colpate or inaperturate, with exine reticulate; ovary sessile, smooth and puberulous or villose externally, ovules in multiple series on each placenta, stigma rhombic or lanceolate, glabrous; disk annular. Capsules elliptic, inflated or flattened, straight or curved, woody, with valves 2, puberulous to villose, without lenticels, with or without glands, without wings, smooth or with ridges, tuberculate, and/or echinate, with calyx caducous; seeds winged (wings reduced), with body papillate or densely pubescent, wings opaque or hyaline, linear. Figures 6, 7.

Number of species, distribution, and habitat. *Amphilophium* includes 47 species found in wet to dry forest, savanna, campinas, and thorn scrub vegetation from Mexico and the Antilles to Argentina and southern Brazil.

Amphilophium is circumscribed here much more broadly than by previous authors to include several previously separated genera, in particular *Haplolophium*, *Glaziova*, *Distictis*, *Distictella*, and *Pithecoctenium*. In this new circumscription *Amphilophium* can be recognized vegetatively by its trifid tendrils terminating in adhesive disks (a synapomorphy of the genus) and the elliptic foliaceous prophylls of the axillary buds that are developed in most species. In flower, *Amphilophium* can be recognized by the coriaceous, cupular, densely pubescent and glandular calyx that is frequently unusual in being doubled or divided distally into two concentric rims, together with the coriaceous corolla that is externally

pubescent and has glands clustered close to the margins. The corollas are adapted for pollination by large and mid-sized bees, including Xylocopid bees, which are typical nectar thieves of other Bignonieae that have thinner-textured corollas that those bees can penetrate more easily (Gentry, 1990). In fruit, *Amphilophium* is immediately recognizable by the seeds with a pubescent or papillate seed coat (Fig. 4C, D), another synapomorphy of the genus. The only other species with a similarly glandular calyx plus a thick-textured corolla is *Tanaecium tetragonolobum* (Jacq.) L. G. Lohmann. However, *T. tetragonolobum* can be separated from *Amphilophium* by its stems with four phloem wedges and its bromeliad-like prophylls on the axillary buds.

The close relationship between *Amphilophium*, *Distictella*, *Glaziova*, *Haplolophium*, *Neves-armondia*, *Pithecoctenium*, and *Urbanolophium* was first noted by Melchior (1927), who placed these seven genera into his subtribe Pithecocteniinae. However, he did not include *Distictis* here, even though it shares several of the characters of his Pithecocteniinae. The genera of Melchior's Pithecocteniinae plus *Distictis* are well characterized morphologically and form a monophyletic group in this present analysis (Fig. 8). The circumscription of genera within this group has long been controversial because the genera have been characterized by combinations of characters, with the individual characters each found in several of the genera. For example, as illustrated in Figure 8, *Distictella* has been diagnosed by the combination of cylindrical stems (also present in species of *Glaziova*), glands grouped at the axils of leaflets (also present in species of *Distictis* and *Pithecoctenium*), corollas bent at a 90° angle above the base (Fig. 7P; also present in *Glaziova* and *Pithecoctenium*), a cupular, truncate, densely pubescent calyx with glands clustered near the margin (Fig. 7P; also found in *Distictis* and *Pithecoctenium*), fruits curved and glandular (often found in species of *Distictis*), and a papillate seed body (also found in some species of *Distictis*). The diagnostic characters of the other genera of Pithecocteniinae are similarly overlapping; for example, *Amphilophium*, *Haplolophium*, and *Glaziova* were all distinguished in part by the distinctive double calyx (Fig. 7B, E), thyrsoid inflorescences, and colpate pollen, and then were separated from each other based on the bilabiate corolla that remains closed at anthesis in *Amphilophium* (Fig. 7B), the cylindrical stems of *Glaziova*, and the hexagonal stems of *Haplolophium*. The similarity among these genera was noted by Gentry (1976: 55): "*Haplolophium* is intermediate between *Pithecoctenium* and *Amphilophium*, agreeing with the former in its tubular bent corollas, simple calyx, and echinate fruit, and with the latter in its pollen, trifid tendrils, dendroid trichomes, and the presence of a frilly calyx margin." Similarly, *Distictis* and *Pithecoctenium* share racemose inflorescences (also found in *Distictella*), villose and lepidote ovaries (also found in *Haplolophium*), and inaperturate pollen (also found in *Distictella*). However, *Pithecoctenium* was separated based on its echinate fruits (Fig. 7I), even though not all species of *Pithecoctenium* have echinate fruits (Pool, 2007a). *Phaedranthus* was initially considered related to *Pithecoctenium*, even though its fruit was unknown; later Gentry (1979: 237) concluded that "the fruit of *Phaedranthus* is very close to that of *Distictis* but only remotely similar to that of *Pithecoctenium*."

The phylogeny hypothesis of the tribe Bignonieae (Lohmann, 2006; Fig. 2) groups all of these genera in a single, strongly supported monophyletic clade that is characterized by several morphological synapomorphies (Fig. 8). This analysis also suggests that this clade comprises two subclades, one composed of *Distictella* and the other including the remaining genera of the Pithecocteniinae. In this second subclade, there are three groups that are generally distinguishable by morphology, though their characterization is incomplete (Fig. 8). These are *Distictis*, *Pithecoctenium*, and the double-calyx group, which includes *Amphilophium* s. str., *Haplolophium*, and *Glaziova*. However, *Distictis* and *Pithecoctenium* individually cannot be characterized by any single morphological synapomorphy, making the taxonomic recognition of the double-calyx group impractical because this would require recognition of both *Distictis* and *Pithecoctenium*. Therefore, a broader generic circumscription is more appropriate, because it leads to a better characterized and recognizable genus morphologically, and because it is more informative regarding the actual patterns of morphological variation and relationships in this group. Therefore a broadly circumscribed *Amphilophium* is here characterized by multiples of four phloem wedges; dimorphic juvenile growth; foliaceous glandular prophylls of the axillary buds; trifid to multifid tendrils; a calyx that is coriaceous, cupular, truncate, and villose and has glands in fields next to the margins; corollas that are generally white, curved, and villose externally and have glands clustered next to the margins; fruits that are elliptic, woody, generally glandular, and tuberculate or echinate; and papillate or pubescent seeds (Fig. 4C, D).

1. Amphilophium arenarium (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Distictella arenaria* A. H. Gentry, Mem.

New York Bot. Gard. 29(1): 273. 1978. TYPE: Venezuela. Amazonas: 18 km S of Samarapo towards Río Sipapo, 125 m, roadside, 29 June 1975, *A. H. Gentry & P. Berry 14615* (holotype, MO-2420903!; isotypes, NY [barcode] NY00328773!, VEN not seen).

Habitat and distribution. This species is found in shrubby and riparian lowland vegetation (Gentry, 1997) in Colombia (Vaupés, Vichada) and Venezuela (Amazonas, Bolívar).

2. Amphilophium aschersonii Ule, in Urb. & Graeb., Festschr. Aschers. 549. 1904. TYPE: Peru. Loreto: Iquitos, Apr. 1903, *E. Ule 6813* (holotype, HBG not seen, HBG as photo F neg. 18445 at MO-1692825!; isotype, K!).

Habitat and distribution. This species is found in humid lowland to montane forest vegetation (Gentry, 1997) in Colombia (Caquetá, Meta), Venezuela (Amazonas, Barinas, Táchira), Ecuador, Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas).

3. Amphilophium bauhinioides (Bureau ex Baill.) L. G. Lohmann, comb. nov. Basionym: *Glaziova bauhinioides* Bureau ex Baill., Hist. Pl. 10: 38. 1888, as "*Glaziovia*." *Glaziovia bauhiniopsis*, orth. var. *Amphilophium bauhinioides* (Bureau ex Baill.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Rio de Janeiro: Gávea, Quatro-Patacas, 26 Apr. 1870, *A. Glaziou 651* (lectotype, designated here, P [barcode] P00481537!; isolectotypes, BR [barcode] BR00880346!, BR [barcode] BR00880379!, MO-2762336!, F-997872 image!, P [barcode] P00481538!).

Nomenclatural note. Baillon (1888) cited as the type of *Glaziova bauhinioides* a collection made by Glaziou in Brazil, but did not list a collection number or herbarium. Hence, the best material deposited at the P herbarium that matches the locality and species described by Baillon is here chosen as a lectotype.

Habitat and distribution. This species is found in wet areas of Altantic forest vegetation in eastern Brazil (Bahia, Distrito Federal, Espírito Santo, Minas Gerais, Rio de Janeiro).

4. Amphilophium blanchetii (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 210. 1896. *Haplolophium blanchetii* DC., in A. DC., Prodr. 9: 192. 1845. TYPE: Brazil. Bahia: Rio São Francisco, Serra de Açuruá, 1839, *J. S. Blanchet 2849* (holotype, G-DC!, G-DC as photo F neg. 7659 at MO-1692958!; isotypes, G-14127!, G-14109!, NY-313079!, P [barcode] P00481499!, P as photocopy at MO-2294584!, MO-3841405!).

Habitat and distribution. This species is found in forest vegetation in eastern Brazil (Bahia).

5. Amphilophium bracteatum (Cham.) L. G. Lohmann, comb. nov. Basionym: *Haplolophium bracteatum* Cham., Linnaea 7: 556. 1832 [1833]. *Amphilophium bracteatum* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1582. 2008, nom. nud. invalid. *Amphilophium bracteatum* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. São Paulo: meridional portion of the state, s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18441 at MO-1692757!, MO-2495171!, NY-328853!).

Habitat and distribution. This species is found in forest vegetation in eastern and southeastern Brazil (Goiás, Minas Gerais, Paraná, Rio de Janeiro, São Paulo).

6. Amphilophium buccinatorium (DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium buccinatorium* DC., in A. DC., Prodr. 9: 195. 1845. *Pithecoctenium buccinatorium* var. *subinclusum* DC., in A. DC., Prodr. 9: 195. 1845, nom. illeg. superfl. *Phaedranthus buccinatorius* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 182. 1863, as "*buccinatorum*." *Bignonia buccinatoria* (DC.) Mairet ex Hemsl., Biol. Cent.-Amer., Bot. 2: 490. 1882. *Distictis buccinatoria* (DC.) A. H. Gentry, Brittonia 25(3): 237. 1973, as "*buccinatorum*." TYPE: Mexico. s. loc., 1833, *M. Mairet de la Chaudefont s.n.* (lectotype, selected by Pool [2007a: 802], G-DC!, G-DC as photo F neg. 7655 at MO-1693024!).

Habitat and distribution. This species is found on rocky outcrops at 1700–2300 m in Mexico (Chiapas, Guanajuato, Jalisco, México, Morelos, Puebla, San Luis Potosí, Tlaxcala; Pool, 2007a).

7. Amphilophium campinae (A. Samp.) L. G. Lohmann, comb. nov. Basionym: *Distictella campinae* A. Samp., Ann. Acad. Brasil. Sci. 7: 120. 1935. TYPE: Brazil. Pará: campinas near Vigia, 21 June 1927 [26 June 1926], *A. Ducke s.n. RB-22688* (holotype, RB-22688!, RB-22688

as photo K neg. 4699 at K!; isotype, MO-2192053!).

Habitat and distribution. This species is known from savanna and campinas vegetation on white sand substrates in Brazilian Amazonia (Amazonas, Pará, Rôndonia; Pool, 2009).

8. Amphilophium carolinae (Lindl.) L. G. Lohmann, comb. nov. Basionym: *Bignonia carolinae* Lindl., Edward's Bot. Reg. 28: sub tab. 45. 1842. *Pithecoctenium carolinae* (Lindl.) G. Nicholson, Ill. Gard. Dict. 3: 152. 1886. TYPE: from cultivated material at Melbury, Lord Ilchester's seat in Dorsetshire [England], 1842, *s. coll. s.n.* (holotype, CGE not seen).

Nomenclatural note. The taxonomy of this species follows Pool (2007a), who synonymized *Pithecoctenium cynanchoides* DC. under this older name based on exemplary taxonomic detective work. This species has sometimes been incorrectly called "Amphilophium cynanchoides," but this latter name is not validly published (e.g., Arbo & Lohmann, 2008).

Habitat and distribution. This species is known from dry forests, thorn scrub, and disturbed vegetation in southern Bolivia, Paraguay, western Uruguay, and Argentina (Chaco, Corrientes, Santiago del Estero, Tucumán; Pool, 2007a).

9. Amphilophium chocoense (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Distictella chocoensis* A. H. Gentry, Phytologia 47(2): 100. 1980. TYPE: Colombia. Chocó: ca. 10 km W of River Quito on Pan American Hwy. (under construction), W of Las Animas, 110 m, 12 Jan. 1979, *A. H. Gentry & E. Renteria 24089* (holotype, COL-232359 image!; isotypes, MO-2717216!, MO-2717217!).

Habitat and distribution. This species is found in lowland wet forest vegetation in western Colombia (Chocó, Valle del Cauca; Pool, 2009).

10. Amphilophium cremersii (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Distictella cremersii* A. H. Gentry, Phytologia 46(4): 209. 1980. TYPE: French Guiana. Along River Tampoc, close to River Alice, 1 Apr. 1977, *G. Cremers 4589* (holotype, MO-2589099!; isotypes, CAY!, P [barcode] P00468594!).

Habitat and distribution. This species is found in riparian forest, at least sometimes on white sand substrates, in Suriname, French Guiana, and Brazil (Pará; Pool, 2009).

11. Amphilophium crucigerum (L.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Bignonia crucigera* L., Sp. Pl. 2: 624. 1753. *Anisostichus crucigera* (L.) Bureau ex Small, Man. S. E. Fl. 1240. 1933. *Pithecoctenium crucigerum* (L.) A. H. Gentry, Taxon 24(1): 123. 1975. TYPE: Morison, Plantae Historiae pars tertia, Oxford s. 15, tab. 3, fig. 6. 1699 (lectotype, designated by Barrie et al. [1991: 265]).

Habitat and distribution. This species is found in semideciduous to evergreen forest and disturbed vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Colima, Guanajuato, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatán), the Greater Antilles (Cuba, Jamaica), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Cauca, Chocó, La Guajira, Madgalena, Nariño, Sucre, Valle del Cauca), Venezuela (Anzoátegui, Apure, Aragua, Barinas, Carabobo, Cojedes, Guárico, Lara, Mérida, Miranda, Portuguesa, Táchira, Zulia), Trinidad and Tobago, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cajamarca, Cusco, Huánuco, Junín, Loreto, Madre de Dios, San Martín), Bolivia, Paraguay, Brazil (Acre, Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, São Paulo, Rio Grande do Sul), Uruguay, and Argentina (Corrientes, Jujuy, Misiones, Salta).

12. Amphilophium cuneifolium (DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium cuneifolium* DC., in A. DC., Prodr. 9: 196. 1845. *Distictella cuneifolia* (DC.) Sandwith, Kew Bull. 8(4): 476. 1953 [1954]. *Amphilophium cuneifolium* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Pará: s. loc., s.d., *Anonymous s.n.* (holotype, P [barcode] P00468595!; isotype, G-DC!).

Habitat and distribution. This species is found in savanna vegetation, at least sometimes in seasonally inundated sites on black soil substrates, in northern Bolivia (Pool, 2009).

13. Amphilophium dasytrichum (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Distictella dasytricha* Sandwith, Kew Bull. 8(4): 476. 1953 [1954]. TYPE: Brazil. Goiás: Queixada, Jataí, 8 July 1949, *A. Macedo 1906* (holotype, K!; isotypes, G!, MO-1622581!, NY

[barcode] NY000328774!, US-2196739 image!, US-2196740 image!, US-2168886 image!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in northern Bolivia and Brazil (Acre, Goiás) (Pool, 2009).

14. Amphilophium dolichoides (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia dolichoides* Cham., Linnaea 7: 696. 1832 [1833]. *Pithecoctenium dolichoides* (Cham.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 218. 1894. *Amphilophium dolichoides* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1583. 2008, nom. nud. invalid. *Amphilophium dolichoides* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *F. Sellow 332* (holotype, LE not seen; isotype, B†, B as photo F neg. 18484 at MO-1692888!).

Nomenclatural note. Pool (2007a: 635) cited the holotype specimen of *Bignonia dolichoides* Cham. as the Sellow specimen identified as such at B, which was destroyed, but did not lectotypify this name. However, Chamisso's original materials are mainly deposited at LE, including a specimen set collected by Sellow in Brazil, and the holotype is expected to be there, but those collections have not yet been studied in detail.

Habitat and distribution. This species is found in Atlantic forest vegetation in Brazil (Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo; Pool, 2007a).

15. Amphilophium dusenianum (Kraenzl.) L. G. Lohmann, comb. nov. Basionym: *Haplolophium dusenianum* Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 118. 1921. *Urbanolophium dusenianum* (Kraenzl.) Melch., Repert. Spec. Nov. Regni Veg. Beih. 46: 81. 1927. *Urbaniella duseniana*, orth. var. TYPE: Brazil. Paraná: Capão Grande, 25 Apr. 1909, *P. Dusén 8015* (lectotype, designated by Melchior [1927: 81], S not seen; isolectotypes, BM not seen, MO-931681!).

Pithecoctenium glaziovii Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 218. 1894, non *Amphilophium glaziovii* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 222. 1894. *Distictis glaziovii* (Bureau ex K. Schum.) Bureau & K. Schum., Fl. Bras. 8(2): 180. 1896. *Urbanolophium glaziovii* (Bureau ex K. Schum.) Melch., Repert. Spec. Nov. Regni Veg. Beih. 46: 80. 1927. *Bothriopodium glaziovii* (Bureau ex K. Schum.) Rizzini, Arch. Jard. Bot. Rio de Janeiro 9: 71. 1949. *Haplolophium glaziovii* (Bureau ex K. Schum) A. H. Gentry, Novon 2(2): 164. 1992. *Amphilophium neoglaziovii* L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Rio de Janeiro, Serra dos Orgãos, s.d., *J. Saldanha 7445* (lectotype, selected by Melchior [1927: 81], B†; isolectotypes, K!, P [barcode] P00481539!).

Nomenclatural note. The oldest name for this species is *Pithecoctenium glaziovii*, but that name cannot be transferred to *Amphilophium* because the name *A. glaziovii* has already been published for another species and thus cannot be used for this species. The published name *Haplolophium dusenianum* also applies to this species and is the next oldest name for it, therefore the combination *A. dusenianum* is made here for this species. The protologue of *H. dusenianum* cited four syntype specimens, *Dusén 8015*, *Dusén 7207*, *Dusén 9493*, and *Dusén 7914*. Melchior (1927) subsequently listed the collection *Dusén 8015* at S as the type of this name, effectively lectotypifying it. Gentry (1992a: 165) later apparently intended to designate the specimen *Dusén 8015* at BM as the lectotype of *H. dusenianum* Kraenzl., without explicit discussion and apparently without realizing that Melchior previously lectotypified this name, but Melchior's choice seems to have priority. Also Gentry (1992a: 165) cited the name *Urbanolophium dusenianum* (Kraenzl.) Melch. incorrectly as "*Urbaniella duseniana* (Kraenzl.) Dusén ex Melch.," with the genus incorrectly spelled and with Dusén added as an author; Melchior, however, did not credit Dusén as an author in his original publication of this combination. No specimens were cited in the protologue of *Pithecoctenium glaziovii* Bureau ex K. Schum., but two specimens were cited by Bureau and Schumann (1896) in their contemporaneous and more detailed treatment, *Saldanha 7445* and *Glaziou 17705*. Melchior chose the first of these as the lectotype, without explanation. Gentry later (1992a: 165) cited *Saldanha 7445* simply as the type of this name, and apparently overlooked Melchior's lectotypification here also. Melchior's lectotype has since been destroyed; further study is needed before a new lectotype is chosen.

Habitat and distribution. This species is found in Atlantic forest vegetation in Brazil (Goiás, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina).

16. Amphilophium ecuadorense A. H. Gentry, Phytologia 35(3): 183. 1977. TYPE: Ecuador. Guayas: Cerro Bella Vista near Julio Moreno, 29 Aug. 1965, *C. Játiva & C. Epling 974* (holotype, NY-82782!; isotypes, MO-2376674!, S not seen, S as photocopy at MO-2376674!).

Habitat and distribution. This species is found in dry forest vegetation in western Ecuador and northwestern Peru (Cajamarca, Piura, Tumbes).

17. Amphilophium elongatum (Vahl) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Bignonia elongata* Vahl, Eclog. Amer. 2: 45, tab. 16. 1798. *Pithecoctenium elongatum* (Vahl) Klotzsch, in M. R. Schomb., Reis. Br.-Guiana 3: 1158. 1848 [1849]. *Doxantha elongata* (Vahl) Miers, Proc. Roy. Soc. London 3: 190. 1863. *Distictis elongata* (Vahl) Bureau ex Benth., Gen. Pl. 2: 1038. 1876. *Distictella elongata* (Vahl) Urb., Repert. Spec. Nov. Regni Veg. 14: 310. 1916. TYPE: French Guiana. Cayenne, s.d., *J. P. von Rohr 2001* (lectotype, designated by Gentry [1983a: 174], C not seen, C as photo F neg. 22130 at MO-1693028!).

Habitat and distribution. This species as circumscribed by Pool (2009), who is followed here, is found in lowland secondary forest vegetation, frequently on white sand substrates, in Suriname, French Guiana, and Brazil (Amazonas, Pará, Rôndonia).

18. Amphilophium falcatum (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia falcata* Vell., Fl. Flumin. 245. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 17. 1827 [1831]. *Pithecoctenium falcatum* (Vell.) A. Pool, Ann. Missouri Bot. Gard. 94(3): 635, fig. 2. 2007. *Amphilophium falcatum* (Vell.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1583. 2008, nom. nud. invalid. *Amphilophium falcatum* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: tab. 17 in Vellozo, Fl. Flumin. Icon. 6, pro parte, including branchlet, leaves, fruits, seeds, 1827 [1831] (lectotype, selected by Pool [2007a: 635]); Brazil, Bahia, Coaraci, Almandina, 18 km de estrada, 5 Feb. 1970, *T. S. dos Santos 574* (epitype, designated by Pool [2007a: 635], MO-2627389!; duplicates, CEPEC not seen, NY not seen).

Nomenclatural note. Pool (2007a: 636, fig. 2) reprinted Vellozo's plate from the protologue of this *Bignonia falcata* and designated part of this as the lectotype of this name but explicitly excluded the inflorescence and flowers of that illustration. She considered this plate to be a composite drawing, with the inflorescence and flowers belonging to a different species in a different genus that she did not identify.

Habitat and distribution. This species is found in disturbed humid vegetation and Atlantic forest vegetation in eastern Bolivia and Brazil (Bahia, Goiás, Minas Gerais, Paraná, Rio de Janeiro, São Paulo).

19. Amphilophium frutescens (DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium frutescens* DC., in A. DC., Prodr. 9: 196. 1845. *Distictis frutescens* (DC.) A. Pool, Ann. Missouri Bot. Gard. 94 (4): 804. 2007. *Amphilophium frutescens* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., 1832, *J. Lhotsky s.n.* (holotype G-DC!, G-DC as photo F neg. 7651 at MO-1693029!; isotype, F not seen).

Nomenclatural note. The names *Pithecoctenium frutescens* DC. and *P. stipulare* Mart. ex DC. were published simultaneously, and both apply to the same species. Pool (2007b) first synonymized these and chose the name *P. frutescens* for nomenclatural reasons. Prior to that, the names *P. stipulare* and *Distictis stipularis* (Mart. ex DC.) A. H. Gentry were more widely used for this species.

Habitat and distribution. This species is found in wet areas of Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Minas Gerais, Paraíba, Rio de Janeiro).

20. Amphilophium glaziovii Bureau ex K. Schum., Nat. Pflanzenfam 4(3b): 222. 1894. TYPE: Brazil: Rio de Janeiro, Santo Antônio, 23 Mar. 1872, *A. Glaziou 5782* (holotype, B†, B as photo F neg. 18446 at MO-1692826!; isotypes, BR not seen, F not seen, MO-2294582!, P [2] not seen, P as photocopies at MO-2295482!, MO-2294583!, and MO-2616850!, S not seen, US-1706131 image!].

Nomenclatural note. More study is needed before the typification of this species can be resolved.

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Minas Gerais, Rio de Janeiro).

21. Amphilophium gnaphalanthum (A. Rich.) L. G. Lohmann, comb. nov. Basionym: *Bignonia gnaphalantha* A. Rich., Hist. Fis. Cuba, Bot. 11: 105. 1850. *Distictis gnaphalantha* (A. Rich.) Greenm., Proc. Amer. Acad. Arts 33: 487. 1898. *Distictis gnaphalantha* (A. Rich.) Urb., Repert. Spec. Nov. Regni. Veg. 14: 310. 1916, comb. superfl. TYPE: Cuba. La Habana, s.d., *R. de la Sagra s.n.* (holotype, P not seen; isotypes, P [2], not seen).

Nomenclatural note. Pool (2007b) clarified the identity of the type of *Bignonia gnaphalantha*, and noted that although Urban (1916) has usually been credited with authorship of the combination *Distictis gnaphalantha*, in fact that combination was made previously by Greenman (1898).

Habitat and distribution. This species is found in lowland forest vegetation on limestone substrates in Cuba.

22. Amphilophium granulosum (Bureau & K. Schum.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 270. 2008. *Pithecoctenium granulosum* Klotzsch, in M. R. Schomb., Reis. Br.-Guiana 3: 1158. 1848 [1849], nom. nud invalid. *Distictis granulosa* Bureau & K. Schum., Fl. Bras. 8(2): 179. 1896. *Distictella granulosa* (Bureau & K. Schum.) Urb., Repert. Spec. Nov. Regni Veg. 14: 310. 1916. *Pithecoctenium granulosum* (Bureau & K. Schum.) Sprague & Sandwith, Bull. Misc. Inform. Kew 1932: 89. 1932. *Anomoctenium granulosum* (Bureau & K. Schum.) Sandwith, Kew Bull. 19: 413. 1965. TYPE: British Guiana [Guyana]. s. loc., s.d., *M. Rich. Schomburgk 400* (holotype, B†); Guyana, s. loc., s.d., *Rob. H. Schomburgk 229 S* (neotype, designated by Pool [2007b: 807], K [barcode] K000195692).

Nomenclatural note. Pool (2007b) noted that the type of *Distictis granulosa*, *M. Rich Schomburgk 400*, was deposited at B and has been destroyed, and that although Gentry (1983a) cited a duplicate of that collection at K, this has not subsequently been located and is presumed either lost or an erroneous report, and no other duplicates of that collection have been located. Accordingly, she designated a neotype, which was selected from extant specimens cited by Sprague and Sandwith (1932).

Habitat and distribution. This species is found in moist to wet forest and disturbed vegetation, sometimes on white sand substrates, in Colombia (Vaupés), Venezuela (Amazonas, Apure, Bolívar), Suriname, French Guiana, Peru (Madre de Dios, Puno), Bolivia, and Brazil (Acre, Amazonas, Maranhão, Pará, Roraima).

23. Amphilophium lactiflorum (Vahl) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Bignonia lactiflora* Vahl, Symb. Bot. 3: 80, tab. 66. 1794. *Distictis lactiflora* (Vahl) DC., in A. DC., Prodr. 9: 191. 1845. *Macrodiscus lactiflorus* (Vahl) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 216. 1894, as "*lactiflora*." TYPE: U.S. Virgin Islands: St. Croix, Paxacam, July, *F. A. F. C. West s.n.* (holotype, C not seen; isotypes, BM-578580!, W!).

Habitat and distribution. This species is found in dry forest and scrub vegetation, often on limestone substrates, in the Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Rico) and the U.S. Virgin Islands (St. Croix, St. Thomas).

24. Amphilophium laeve (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008, as "*laevis*." *Distictella monophylla* Sandwith var. *laevis* Sandwith, Mem. New York Bot. Gard. 9(3): 362. 1957. *Distictella laevis* (Sandwith) A. H. Gentry, Mem. New York Bot. Gard. 29(1): 274. 1978. TYPE: Venezuela. Amazonas: Cerro Yapacana, Río Orinoco, Savanna no. 1, along trail to gold mine camp, 100 m, 7 Jan. 1951, *B. Maguire, R. S. Cowan & J. J. Wurdack 30788* (holotype, NY [barcode] NY00328776!).

Habitat and distribution. This species is found in shrubby campinas or savanna vegetation on white sand substrates (Gentry, 1997) in Venezuela (Amazonas) and Brazil (Amazonas, Pará).

25. Amphilophium laxiflorum (DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium laxiflorum* DC., in A. DC., Prodr. 9: 195. 1845. *Distictis laxiflora* (DC.) Greenm., Proc. Amer. Acad. Arts 33: 486. 1898. TYPE: Mexico. Oaxaca: s. loc., July, *G. Andrieux 220* (holotype, G-DC!; isotypes, M not seen, W not seen).

Nomenclatural note. The names *Pithecoctenium laxiflorum* and *P. cinereum* DC. were published simultaneously and were synonymized by Standley (1926) under the name *P. laxiflorum*.

Habitat and distribution. This species is found in deciduous forest vegetation and rocky areas at 1100–2000 m in Mexico (Chiapas, Guanajuato, Jalisco, Oaxaca, Puebla, Veracruz) and Nicaragua (Pool, 2007b), and is cultivated widely in tropical regions.

26. Amphilophium lohmanniae (A. Pool) L. G. Lohmann, comb. nov. Basionym: *Distictella lohmanniae* A. Pool, Ann. Missouri Bot. Gard. 96(2): 304, fig. 3. 2009. TYPE: Brazil. Amazonas: Reserva Florestal Ducke, Manaus–Itacoatiara [Hwy.], Km. 26, 2°53′S, 59°58′W, 20 m, 14 July 1995, *L. G. Lohmann & C. F. da Silva 20* (holotype, MO-6152640!; isotype, INPA!).

Habitat and distribution. This species is found in wet lowland terra firme forest vegetation in Amazonian Brazil (Amazonas).

27. Amphilophium magnoliifolium (Kunth) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Bignonia magnoliifolia* Kunth, Nov. Gen. Sp. 3: 136. 1818 [1819], as "*magnoliaefolia*." *Distictella magnoliifolia* (Kunth) Sandwith, Lilloa 3: 460. 1938. TYPE: Venezuela. Amazonas: prope Javita, ad ripam fluminum Tuamini et Temi (Missiones del Orinoco), May 1800, *F. W. H. A. von Humboldt & A. J. A. Bonpland 973* (lectotype, selected by Sandwith [1938: 460], P-Bonpl.!, P-Bonpl. as photo F neg. 39415 at MO-1692923!).

Habitat and distribution. Pool (2009) circumscribed this species more narrowly than previous authors, and separated many plants formerly included here into *Distictella racemosa* (Bureau & K. Schum.) Urb. In her circumscription, followed here, *Amphilophium magnoliifolium* is known from lowland seasonal forest, scrub, and savanna vegetation, usually on white sand substrates, in Colombia (Guanía, Vaupés), Venezuela (Amazonas), and Brazil (Amazonas).

28. Amphilophium mansoanum (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia mansoana* DC., in A. DC., Prodr. 9: 157. 1845. *Distictis mansoana* (DC.) Bureau ex B. Verl., Rev. Hort. 40: 154. 1868, as "*mensoana*." *Distictella mansoana* (DC.) Urb., Repert. Spec. Nov. Regni Veg. 14: 310. 1916. *Amphilophium mansoanum* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: close to Cuiabá, 1832, *A. Silva Manso s.n.* (holotype, G-DC!).

Habitat and distribution. This species as circumscribed by Pool (2009), who is followed here, is found in moist forest, disturbed, savanna, and gallery forest vegetation in Peru (Madre de Dios, Puno), eastern Bolivia, and Brazil (Amazonas, Bahia, Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Pará, Rôndonia, Roraima, São Paulo).

29. Amphilophium monophyllum (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Distictella monophylla* Sandwith, Mem. New York Bot. Gard. 9(3): 361. 1957. TYPE: Venezuela. Amazonas: Cerro Sipapo (Paráque), Camp Savanna, 1500 m, 15 Dec. 1948, *B. Maguire & L. Politi 27717* (holotype, K not seen; isotype, NY-328775!).

Habitat and distribution. This species is known from savanna vegetation on white sand substrates (Gentry, 1997) in Colombia (Guanía) and Venezuela (Amazonas).

30. Amphilophium nunezii (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Haplolophium nunezii* A. H. Gentry, Novon 2(2): 163, fig. 2. 1992. TYPE: Peru. Madre de Dios: Tambopata, Cuzco Amazónico, Tourist Lodge, 18 May 1989, *P. Nuñez & O. Phillips 10412* (holotype, MO-3732179!; isotypes, CUZ not seen, G!, NY-328854!, USM not seen).

Habitat and distribution. This species is found in lowland wet forest vegetation in Peru (Cusco, Madre de Dios) and Bolivia.

31. Amphilophium obovatum (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Distictella obovata* Sandwith, Mem. New York Bot. Gard. 9: 362. 1957. TYPE: Guyana. Upper Mazaruni River, Kataima, 550 m, 17 Nov. 1951, *B. Maguire & D. B. Fanshawe 32637* (holotype, K!; isotypes, F-1446610 image!, NY-328777!, US-2168886 image!).

Habitat and distribution. This species is found in savanna, disturbed, and forest vegetation, often on white sand substrates, in Venezuela (Bolívar), Guyana, and Brazil (Pará).

32. Amphilophium occidentale (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Distictis occidentalis* A. H. Gentry, Novon 2(2): 161, fig. 1A–B. 1992. TYPE: Colombia. Santander: 3 km N of Yarima on rd. to Albania SE of Barranca Bermeja, 25 July 1975, *A. H. Gentry & L. Forero 15409* (holotype, MO-2340615!; isotype, COL not seen).

Habitat and distribution. This species is found in lowland wet forest vegetation, usually in riverine or seasonally inundated areas, in Colombia (Amazonas, Chocó, Santander), Ecuador, Peru (Amazonas, Cusco, Loreto, Madre de Dios), and eastern Bolivia.

33. Amphilophium paniculatum (L.) Kunth, Nov. Gen. Sp. 3: 149. 1818 [1819]. *Bignonia paniculata* L., Sp. Pl. 2: 623. 1753. *Endoloma purpurea* Raf., Syla Tellur. 80. 1838, nom. illeg. superfl. *Arrabidaea paniculata* (L.) Seem., Trans. Linn. Soc. London 23: 14. 1862. TYPE: Plumier, Pl. Amer., 46, tab. 56, fig. 1, 1756 (lectotype, selected by Howard [1989: 317]).

Habitat and distribution. This species is widely distributed through wet and dry forest vegetation in Mexico (Campeche, Chiapas, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Quintana Roo, San Luis Potosí, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatán), the Lesser Antilles (Dominica, Guadeloupe, Martinique, St. Vincent), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Bolívar, Cundinamarca, Nariño, Risaralda, Sucre, Valle del Cauca), Venezuela (Amazonas, Anzoátegui, Aragua, Barinas, Bolívar, Delta Amacuro, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Portuguesa, Sucre, Yaracuy, Zulia), Trinidad and Tobago, Guyana, Ecuador, Peru (Amazonas, Cajamarca, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Piura, San Martín, Tumbes), Bolivia, Paraguay, Brazil (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Pernambuco, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo), and Argentina (Chaco, Corrientes, Formosa, Jujuy, Misiones, Salta, Tucumán).

34. Amphilophium pannosum (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 209. 1896. *Bignonia pannosa* DC., in A. DC., Prodr. 9: 148. 1845. TYPE: Peru. s. loc., 1778–1788, *H. Ruiz & J. Pavón s.n.* (holotype, G-14110!, G as photo F neg. 26184 at MO-2131606!).

Habitat and distribution. This species is found in wet to dry forest vegetation in Costa Rica, Panama, Colombia (Antioquia, Cauca, Cundinamarca, Santander, Valle del Cauca), Venezuela (Mérida, Táchira), Ecuador, Peru (Cajamarca, Cusco, Loreto, Pasco), Bolivia, and Argentina (Jujuy, Salta).

35. Amphilophium parkeri (DC.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Bignonia parkeri* DC., in A. DC., Prodr. 9: 157. 1845. *Distictella parkeri* (DC.) Sprague & Sandwith, Bull. Misc. Inform. Kew 1932: 90. 1932. TYPE: Guyana. Demerara River, 1826, *Parker s.n.* (holotype, G-DC!, G-DC as photo F neg. 7637 at MO-1692900!; isotype, K!).

Habitat and distribution. This species as circumscribed by Pool (2009), who is followed here, is found in wet forest and disturbed vegetation, often on white sand substrates, widely but apparently not frequently in Colombia (Amazonas), Venezuela (Bolívar), Guyana, Suriname, French Guiana, and Brazil (Amapá).

36. Amphilophium pauciflorum (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Distictella pauciflora* A. H. Gentry, Ann. Missouri Bot. Gard. 61(3): 872. 1974. TYPE: Venezuela. Bolívar: región de Canaima, entre el hotel y el Salto Hacha, 6°15′N, 62°47′W, 400 m, 18 July 1972, *J. A. Steyermark 106343* (holotype, MO-5104409!).

Habitat and distribution. This species is only known from the type collection from eastern Venezuela (Bolívar), and its habitat vegetation type is unknown (Gentry, 1997).

37. Amphilophium perbracteatum A. H. Gentry, Phytologia 57(3): 241. 1985. TYPE: Brazil. Bahia: Serra Geral de Caitité, 9 km S of Brejinhos das Ametistas, 14°19′S, 42°27′W, 900 m, 12 Apr. 1980, *R. M. Harley, G. L. Bromley, A. M. de Carvalho, J. L. Hage & H. S. Brito 21286* (holotype, CEPEC not seen; isotypes, K!, MO-2918680!, MO-3520342!).

Habitat and distribution. This species is only known from the type collection from tall deciduous forest vegetation in eastern Brazil (Bahia).

38. Amphilophium pilosum Standl., Field Mus. Nat. Hist., Bot. Ser. 17(4): 392. 1938, as "*Amphilopium.*" TYPE: Honduras. Comayagua: along river bank on plains near Siguatepeque, 1050 m, 25 July 1936, *T. G. Yuncker, R. F. Dawson & H. R. Youse 6683* (holotype, F-873360 image!, F as unnumbered photo at MO-1183683!; isotype, MO-1167116!).

Habitat and distribution. This species is known from wet forest vegetation in Honduras.

39. Amphilophium porphyrotrichum (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Distictella porphyrotricha* Sandwith, Bol. Soc. Venez. Ci. Nat. 25(106): 48. 1963. TYPE: Venezuela. Bolívar: vic. Km. 135 S of El Dorado, NE of Luepa, in drainage of Río Cuyuni, 800–1200 m, 6–11 Mar. 1962, *J. A. Steyermark & L. Aristeguieta 98* (holotype, K!; isotypes, NY-328779!, US-2430090 image!).

Habitat and distribution. This species is known from wet premontane forest vegetation at 800–1380 m (Pool, 2009) in Venezuela (Bolívar), Brazil (Amapá), and perhaps Guyana.

40. Amphilophium pulverulentum (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Distictella pulverulenta* Sandwith, Brittonia 3(2): 91. 1938. *Distictis pulverulenta* (Sandwith) A. H. Gentry, Ann. Missouri Bot. Gard.

63(1): 77. 1976. TYPE: Brazil. Amazonas: basin of Rio Solimões, São Paulo de Olivença, basin of creek Belém, 26 Oct.–11 Dec. 1936, *B. A. Krukoff 8685* (holotype, NY-328780!; isotypes, BM-603417!, BR!, F-929820 image!, GH not seen, K!, MO-1261554!, P [barcode] P00468596!, U not seen).

Habitat and distribution. This species is found in non-inundated lowland forest and disturbed vegetation, often on white sand substrates, in Colombia (Amazonas, Caquetá, Vaupés), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Peru (Loreto, San Martín), and Brazil (Amazonas).

41. Amphilophium racemosum (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Distictis racemosa* Bureau & K. Schum., Fl. Bras. 8(2): 179. 1896. *Distictella racemosa* (Bureau & K. Schum.) Urb., Repert. Spec. Nov. Regni Veg. 14: 310. 1916. TYPE: Suriname. Wanica River, s.d., *H. R. Wullschlaegel 1033* (lectotype, designated by Pool [2009: 315], BR-880400 not seen).

Habitat and distribution. Pool (2009) circumscribed this species differently than done by previous authors, who have considered it a synonym of *Distictella magnoliifolia*. In her new circumscription, followed here, *Amphilophium racemosum* is found in wet forest vegetation in Colombia (Amazonas, Antioquia, Caquetá, Chocó, Santander, Vaupés), Venezuela (Amazonas, Bolívar, Delta Amacuro, Sucre), Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Junín, Loreto, Madre de Dios, Puno, San Martín), Bolivia, and Brazil (Amazonas, Mato Grosso, Pará, Rôndonia, Roraima).

42. Amphilophium reticulatum (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Distictella reticulata* A. H. Gentry, Ann. Missouri Bot. Gard. 65(2): 728. 1978 [1979]. *Amphilophium reticulatum* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus, Igarapé da Cachoeira Alta do Tarumã, 28 Aug. 1962, *W. Rodrigues & J. Chagas 4610* (holotype, INPA not seen; isotype, MO-2228017!).

Habitat and distribution. This species is known from campinas and riverside vegetation, generally on white sand substrates, in the central Amazon basin near Manaus, Brazil (Amazonas).

43. Amphilophium rodriguesii (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Haplolophium rodriguesii* A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 53, fig. 2. 1976. *Amphilophium rodriguesii* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus, rd. to Igarapé do Passarinho, 22 May 1962, *W. Rodrigues & J. Chagas 4460* (holotype, INPA not seen; isotypes, MO-2232870!, NY-328855!).

Habitat and distribution. This species is found in wet forest vegetation in Panama, Colombia (Amazonas, Córdoba), French Guiana, Bolivia, and Brazil (Amazonas, Pará).

44. Amphilophium sandwithii Fabris, Darwiniana 13(2–4): 456, fig. 3. 1964. TYPE: Argentina. Jujuy: Santa Bárbara, El Fuerte, 1700 m, *H. A. Fabris 5103* (holotype, SI not seen).

Habitat and distribution. This species is found in humid forest vegetation at 1500–2500 m in Bolivia and Argentina (Jujuy, Salta).

45. Amphilophium scabriusculum (Mart. ex DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium scabriusculum* Mart. ex DC., in A. DC., Prodr. 9: 197. 1845. *Distictis scabriuscula* (Mart. ex DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 61(2): 499. 1974. *Amphilophium scabriusculum* (Mart. ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 761. 2010, nom. nud. invalid. TYPE: Brazil. Paraíba: Rio Paraíba, 1826, *Prince Videnses (Wied-Neuwied) s.n.* (holotype, BR-802423!).

Habitat and distribution. This species is found in Atlantic forest vegetation in Brazil (Bahia, Espírito Santo, Minas Gerais, Paraíba, and Pernambuco).

46. Amphilophium stamineum (Lam.) L. G. Lohmann, comb. nov. Basionym: *Bignonia staminea* Lam., Encycl. 1: 421. 1785. *Wunschmannia staminea* (Lam.) Urb., Symb. Antill. 5: 494. 1908. *Distictis staminea* (Lam.) A. H. Gentry, Ann. Missouri Bot. Gard. 61(2): 497. 1974. TYPE: Plumier, Pl. Amer. tab. 56, fig. 2, 1756 (lectotype, designated by de Candolle [1845: 161]).

Habitat and distribution. This species is found in lowland dry forest vegetation in the Greater Antilles, on the island of Hispaniola (Dominican Republic, Haiti).

47. Amphilophium steyermarkii (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 271. 2008. *Distictis steyermarkii* A. H. Gentry, Ann. Missouri Bot. Gard. 61(2): 499. 1974.

TYPE: Venezuela. Distrito Federal: betw. Osma & Todasana, 100 m, 24 Nov. 1971, *J. A. Steyermark & C. B. Carias 105274* (holotype, MO-5104410!; isotypes, MO-2102596!, VEN not seen).

Habitat and distribution. This species is found in deciduous forest vegetation in Colombia (César, Norte de Santander) and Venezuela (Distrito Federal, Miranda, Táchira, Trujillo, Zulia).

III. Anemopaegma Mart. ex Meisn., Pl. Vasc. Gen. 1: 300, 2: 208. 1840, as "*Anemopaegmia*," nom. & orth. cons. TYPE: *Anemopaegma mirandum* (Cham.) Mart. ex DC. [= *Anemopaegma arvense* (Vell.) Stellfeld ex J. F. Souza].

Cupulissa Raf., Fl. Tellur. 2: 57. 1836 [1837], nom. rej. vs. *Anemopaegma* Mart. ex Meisn. TYPE: *Cupulissa grandifolia* (Jacq.) Raf. [≡ *Anemopaegma grandifolium* (Jacq.) Merr. & Sandwith].

Platolaria Raf., Sylva Tellur. 78. 1838, nom. rej. vs. *Anemopaegma* Mart. ex Meisn. TYPE: *Platolaria flavescens* Raf., nom. illeg. superfl. [= *Anemopaegma orbiculatum* (Jacq.) A. DC.].

Pseudopaegma Urb., Ber. Deutsch. Bot. Ges. 34: 739. 1916. TYPE: *Pseudopaegma juncundum* (Bureau & K. Schum.) Urb. (lectotype, designated by Sandwith [1962: 453]) [≡ *Anemopaegma juncundum* Bureau & K. Schum.].

Shrubs or lianas, without dimorphic juvenile growth, without strong odor; stems with phloem wedges in multiples of 4 in cross-section, pith solid; branchlets cylindrical, glabrous to pubescent, with sparsely to densely distributed lenticels, without (with) interpetiolar gland fields, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds elliptic and foliaceous or minute and triangular, with glands. Leaves 2- or 3-(or 5-)foliolate, terminal leaflet often replaced by a trifid (simple) tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous or coriaceous, with glands grouped in axils of veins or sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary, a raceme, fascicle, cyme, or compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular, shortly (deeply) 5-lobed or truncate, membranaceous or coriaceous, glabrous to villose externally, without glands or with glands clustered near margins; corolla yellow (white or red), infundibuliform, straight in tube, membranaceous, puberulous (villose) externally, with nectar guides, with glands arranged in lines on upper portion of tube, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary stipitate, smooth and lepidote externally, ovules in multiple series on each placenta, stigma rhombic, glabrous; disk annular. Capsules elliptic and stipitate, flattened, straight, coriaceous, with valves 2, glabrous (pubescent), without lenticels, without glands, without wings, smooth, with calyx persistent; seeds winged or not, with body smooth and glabrous, wings hyaline or opaque, linear. Figure 9.

Number of species, distribution, and habitat. *Anemopaegma* includes 45 species found in wet to dry forest, savanna, and dry caatinga vegetation from Mexico to Argentina and southern Brazil.

Anemopaegma is highly supported (100%) as monophyletic in the phylogenetic hypothesis of Bignonieae (Lohmann, 2006; Fig. 2), and is well characterized by its generally racemose inflorescences with yellow flowers and glands at the base of the corolla lobes, a glandular calyx, and a stipitate ovary and fruit (Fig. 9D, E; the last two characters are synapomorphies of the genus). Vegetatively, *Anemopaegma* is characterized by cylindrical stems, prophylls of the axillary buds that are foliaceous and elliptic to somewhat orbicular or heart-shaped, the frequent presence of glands in the axils of the secondary veins of leaflets, and trifid tendrils. The genus predominantly has yellow bee-pollinated flowers, with only *A. ionanthum* A. H. Gentry having red flowers and known to be hummingbird-pollinated (Gentry, 1985).

1. Anemopaegma acutifolium DC., in A. DC., Prodr. 9: 188. 1845. TYPE: Brazil. Mato Grosso: s. loc., 1833, *C. Gaudichaud 97* (holotype, P!, P as photo F neg. 39942 at F!; isotypes, G-DC!, R not seen).

Habitat and distribution. This species is found in dry forest and cerrado vegetation in Bolivia and Brazil (Bahia, Distrito Federal, Goiás, Mato Grosso, São Paulo).

2. Anemopaegma alatum A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 67. 1976. TYPE: Venezuela. Sucre: betw. La Sabana, Los Altos & La Silleta, towards Zurita, 600 m, 18 Aug. 1973, *J. A. Steyermark, V. Carreño Espinoza & B. J. Manara 107753* (holotype, MO-2133145!; isotype, VEN not seen).

Habitat and distribution. This species is found in evergreen lowland and lower montane forest vegetation (Gentry, 1997) in Colombia (Vaupés) and Venezuela (Bolívar, Monagas, Sucre).

3. Anemopaegma album Mart. ex DC., in A. DC., Prodr. 9: 188. 1945. TYPE: Brazil. Minas

Gerais: Contendas, Diamantina [sub Tejuco] at Formigas, Aug. 1818, *C. F. P. von Martius 1553* (lectotype, designated here, M-86292!, M as photo F neg. 20452 at MO-1692833!; isolectotypes, G-DC!, M-86293!, M-86293!, M-86295!, M-86294!).

Nomenclatural note. The name *Anemopaegma album* was published simultaneously with *A. quinquedentatum* Mart. ex DC., and these are today considered synonyms; these names were first synonymized by Bureau and Schumann (1896), who chose the first name. Original material of *A. album* is deposited at M, where there are five duplicates of the type. The best material is here chosen as the lectotype.

Habitat and distribution. This species is found in cerrado and carrasco vegetation in eastern Brazil (Bahia, Ceará, Minas Gerais).

4. Anemopaegma arvense (Vell.) Stellfeld ex J. F. Souza, Tribuna Farm. 13: 275. 1945. *Bignonia arvensis* Vell., Fl. Flumin. 250. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 40. 1827 [1831]. *Jacaranda arvensis* (Vell.) Steud., Nomencl. Bot., ed. 2, 1: 795. 1840. TYPE: tab. 40 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in cerrado vegetation in Bolivia, Paraguay, and Brazil (Bahia, Ceará, Distrito Federal, Maranhão, Mato Grosso, Paraná, Rôndonia).

5. Anemopaegma brevipes S. Moore, Trans. Linn. Soc. London, Bot. 4: 420. 1895. TYPE: Brazil. Mato Grosso do Sul: close to Corumbá, *S. Moore 1009* (holotype, BM not seen; isotype, NY-313061!).

Habitat and distribution. This species is found in dry forest vegetation in central Brazil (Goiás, Mato Grosso do Sul).

6. Anemopaegma chamberlaynii (Sims) Bureau & K. Schum., Fl. Bras. 8(2): 128. 1896, as "*chaimberlaynii*." *Bignonia chamberlaynii* Sims, Bot. Mag. 47: tab. 2148. 1820. *Bignonia aequinoctialis* var. *chamberlaynii* (Sims) Ker Gawl., Bot. Reg. 9: tab. 741. 1823. TYPE: tab. 2148 in Sims, Bot. Mag. 47, 1820 (lectotype, designated here).

Anemopaegma scandens (Vell.) Corr. Méllo ex K. Schum., Nat. Pflanzenfam. 4(3b): 215. 1894. *Bignonia scandens* Vell., Fl. Flum. 246. 1825 [1829]; Fl. Flum. Icon. 6: tab. 22. 1827 [1831]. TYPE: tab. 22 in Vellozo, Fl. Flum. Icon. 6, 1827 [1831] (lectotype, designated here).

Nomenclatural note. Sims did not make any reference to a type at the time of publication of *Bignonia chamberlaynii*. No corresponding material has been located, and the illustration presented in Sims' publication is here chosen as the lectotype.

Habitat and distribution. This species is found in dry to wet forest vegetation in Bolivia, Paraguay, and Brazil (Bahia, Ceará, Distrito Federal, Espírito Santo, Mato Grosso do Sul, Minas Gerais, Paraná, Piauí, Rio de Janeiro, São Paulo).

7. Anemopaegma chrysanthum Dugand, Caldasia 4(19): 307. 1947. TYPE: Colombia. Cauca: costa del Pacífico, río Micay, brazo Noanamito, orilla derecha, El Chachajo, 2–5 m, 27 Feb. 1943, *J. Cuatrecasas 14269* (holotype, COL-16368 image!; isotypes, F-1336989 image!, US-2817237 image!).

Habitat and distribution. This species is found in wet to dry lowland forest vegetation in Mexico (Chiapas, Oaxaca, Tabasco, Veracruz), Belize, El Salvador, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Cauca, Chocó, Cundinamarca, Nariño, Quindio, Risaralda, Valle del Cauca), Ecuador, and Peru (Cajamarca, Loreto, Piura, Tumbes).

8. Anemopaegma chrysoleucum (Kunth) Sandwith, Lilloa 3: 459. 1938. *Bignonia chrysoleuca* Kunth, Nov. Gen. Sp. 3: 134. 1818 [1819]. TYPE: Colombia. Bolívar: Río Magdalena, betw. Río Viego [sic] & Bojorque, May, s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland 1576* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 339411 at MO-1692922!).

Habitat and distribution. This species with water-dispersed seeds is found in humid lowland forests, often on riversides (Gentry, 1997), in Mexico (Veracruz), Belize, Guatemala, Honduras, Costa Rica, Nicaragua, Panama, Colombia (Amazonas, Antioquia, Atlántico, Bolívar, Caquetá, Cauca, César, Chocó, Córdoba, Guianía, Magdalena, Meta, Nariño, Putumayo, Valle del Cauca, Vaupés, Vichada), Venezuela (Amazonas, Apure, Barinas, Bolívar, Delta Amacuro, Táchira, Zulia), Trinidad and Tobago, Guyana, Suriname, Ecuador, Peru (Amazonas, Loreto, Madre de Dios, San Martín, Ucayali), Bolivia, and Brazil (Amazonas, Pará).

9. Anemopaegma citrinum Mart. ex DC., in A. DC., Prodr. 9: 189. 1845. TYPE: Brazil. s. loc., s.d., *C. F. P. von Martius s.n.* (lectotype, designated

here, BR-880372!; isolectotypes, BR-880339!, BR-880307!, BR-880303!, BR-880336!).

Nomenclatural note. Part of Martius' herbarium has been transferred to BR; therefore, the specimens there represent original material. There are five duplicates of the type material of this species at BR, and the best material is here chosen as the lectotype.

Habitat and distribution. This species is found in dry forest, carrasco, and cerrado vegetation in eastern Bolivia and Brazil (Bahia, Maranhão, Minas Gerais, Paraiba, Piauí).

10. Anemopaegma colombianum (Sandwith) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 67. 1976. *Pseudopaegma colombianum* Sandwith, Kew Bull. 8(4): 473. 1953 [1954]. TYPE: Colombia. Meta: Villavicencio, Los Llanos, towards El Parrao, 500 m, 10 Nov. 1938, *J. Cuatrecasas 4605* (lectotype, designated here, COL-24928 image!, COL as photo K. neg. 2007 at K!; isolectotype, US-1773513 image!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Cuatrecasas 4605* and *Romero-Castañeda 1513*. Both collections are deposited at COL. The collection *Cuatrecasas 4605* has been photographed by K and the photos distributed for reference, thus this is here selected as the lectotype.

Habitat and distribution. This species is found, apparently infrequently, in wet forest vegetation in Colombia (Antioquia, Meta) and Peru (Loreto, Pasco).

11. Anemopaegma flavum Morong, Ann. New York Acad. Sci 7: 188. 1892. TYPE: Paraguay. On hwy. from Villa Rica to Escoba, 30 Jan. 1889, *T. Morong 567* (holotype, NY-313063!).

Habitat and distribution. This species is found in dry forest vegetation in Peru (Madre de Dios), Bolivia, Paraguay, and Argentina (Chaco, Corrientes, Formosa, Santa Fe).

12. Anemopaegma floridum Mart. ex DC., in A. DC., Prodr. 9: 188. 1845. TYPE: Brazil. Amazonas: Rio Negro, Rio Japurá, s.d., *C. F. P. von Martius s.n.* (holotype, M-86304!, M as photo F neg. 20453 at MO-1692835! and at INPA!; isotype, M-86305!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Caquetá, Vaupés), Venezuela (Amazonas), Ecuador, Peru (Loreto, Madre de Dios), Bolivia, and Brazil (Acre, Amazonas, Bahia, Espírito Santo, Maranhão, Mato Grosso, Minas Gerais, Piauí, Rio de Janeiro, Rôndonia).

13. Anemopaegma foetidum Bureau & K. Schum, Fl. Bras. 8(2): 143. 1896. TYPE: Brazil. Amazonas: Alto Amazonas, Manaus, 20 Apr. 1882, *C. Schwacke 3620* (holotype, B†, B as photo F neg. 18454 at MO-1692836!).

Nomenclatural note. The type of this species was deposited at B and subsequently was destroyed, and no isotypes have so far been located. Ongoing monographic work will clarify the typification of this species (Firetti-Leggieri & Lohmann, in prep.).

Habitat and distribution. This species is found in wet forest and campinarana vegetation in Colombia (Vaupés), Guyana, Suriname, and Brazil (Amazonas, Pará).

14. Anemopaegma glaucum Mart. ex DC., in A. DC., Prodr. 9: 188. 1845. TYPE: Brazil. Minas Gerais: close to Chapada of Paranan, "in Taboleiro ao fl. Formoso," Sep. 1818, *C. F. P. von Martius 1823* (lectotype, designated here, M-86307!; isolectotypes, G-DC!, G-DC as photo F neg. 7664 at MO-1692837!, M-86309!, M-86308!).

Nomenclatural note. The names *Anemopaegma glaucum* and *A. lanceifolium* DC. were published simultaneously and are today considered synonyms. These were first synonymized by Bureau and Schumann (1896), who chose the name *A. glaucum*. Original material of *A. glaucum* is deposited at M, where there are four duplicates of the type collection. The best material is here chosen as the lectotype.

Habitat and distribution. This species is found in cerrado vegetation in Bolivia, Paraguay, and Brazil (Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, São Paulo).

15. Anemopaegma goyazense K. Schum., Fl. Bras. 8(2): 407. 1896 [1897]. TYPE: Brazil. Goiás: Fazenda da Bolívia, 1894–1895, *A. Glaziou 21846* (holotype, B†, B as photo F neg. 18455 at MO-1692838!; lectotype, designated here, K [barcode] K000449381!; isolectotypes, BR-880306!, F-998948 image!, F-998948 as photo F neg. 18455 at INPA!, G-14111!).

Nomenclatural note. The type of this species was apparently destroyed at B, and no material was found

at P where Bureau worked. The isotype seen with the best material is here designated as the lectotype.

Habitat and distribution. This species is found, apparently infrequently, in cerrado and dry carrasco vegetation in east-central Brazil (Bahia, Goiás, Minas Gerais).

16. Anemopaegma gracile Bureau & K. Schum., Fl. Bras. 8(2): 132. 1896. TYPE: Brazil. Rio de Janeiro: Nova Friburgo, Alto da Boa Vista, 22 Mar. 1880, *A. Glaziou 12999* (holotype, P [barcode] P00468583!, P as photocopy at MO-2294617!; isotype, K!, K as photocopy at MO-2904350!).

Habitat and distribution. This species is found infrequently in dry to wet forest vegetation in east-central Brazil (Distrito Federal, Goiás, Minas Gerais, Rio de Janeiro) and in northeastern Brazil (Pernambuco).

17. Anemopaegma grandifolium (Jacq.) Merr. & Sandwith, J. Arnold Arbor. 28: 432. 1947. *Bignonia grandifolia* Jacq., Pl. Hort. Schoenbr. 3: 19, tab. 287. 1789. *Cupulissa grandifolia* (Jacq.) Raf., Fl. Tellur. 2: 57. 1836 [1837]. TYPE: tab. 287 in Jacquin, Pl. Hort. Schoenbr. 3: 1789 (lectotype, designated here).

Habitat and distribution. This species is found in humid evergreen vegetation in northern Venezuela (Distrito Federal, Mérida, Miranda).

18. Anemopaegma granvillei A. H. Gentry, Ann. Missouri Bot. Gard. 64(2): 311. 1977 [1978]. TYPE: French Guiana. Rivière Petite Ouaqui vers l'embouchere de la crique Carbet Brûle, 27 July 1973, *J. J. de Granville 1935* (holotype, CAY not seen; isotypes, CAY not seen, MO-2665614!).

Habitat and distribution. This species is only known from the type specimen, from wet forest vegetation in southern French Guiana.

19. Anemopaegma heringeri J. C. Gomes, Arch. Jard. Bot. Rio de Janeiro 12: 147. 1953. TYPE: Brazil. Minas Gerais: Coronel Pacheco, Estação Experimental, 3 Dec. 1942, *E. P. Heringer 1147* (holotype, RB-76935 [barcode] 642332!; isotype, MO-2192050!, RB-76935 [barcode] 284908!).

Habitat and distribution. This species is known from dry forest vegetation in southeastern Brazil (Minas Gerais).

20. Anemopaegma hilarianum Bureau & K. Schum., Fl. Bras. 8(2): 124, tab. 80. 1896. TYPE: Brazil. Rio de Janeiro: Petrópolis, 19 Jan. 1876, *A. Glaziou 4105* (holotype, P [barcode] P00468585!, P as photocopy at MO-2294581!; isotypes, C not seen, C as photo F neg. 22139 at MO-1692839!).

Habitat and distribution. This species is found in forest vegetation in southeastern Brazil (Bahia, Goiás, Minas Gerais, Rio de Janeiro).

21. Anemopaegma insculptum (Sandwith) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 67. 1976. *Pseudopaegma insculptum* Sandwith, Kew Bull. 9: 608. 1954 [1955]. TYPE: Colombia. Amazonas: Río Caquetá, La Pedrera, 240 m, 1–4 Oct. 1952, *H. García-Barriga 14617* (holotype, K!; isotypes, COL-407593 image!, MO-04922799!, US-2144508 image!, US-3362853 image!).

Habitat and distribution. This species is found in wet forest vegetation in Colombia (Amazonas), Peru (Madre de Dios, Puno), Bolivia, and Brazil (Amazonas, Rôndonia).

22. Anemopaegma ionanthum A. H. Gentry, Phytologia 57(3): 242. 1985. TYPE: French Guiana. Nord: Massif des Emerillons, 300 m, 20 Sep. 1980, *G. Cremers 6737* (holotype, MO-2887201!; isotype, CAY not seen).

Habitat and distribution. This species is found in wet forest vegetation in Guyana, French Guiana, and northern Brazil (Amapá, Amazonas, Pará).

23. Anemopaegma jucundum Bureau & K. Schum., Fl. Bras. 8(2): 144. 1896. *Pseudopaegma jucundum* (Bureau & K. Schum.) Urb., Ber. Deutsch. Bot. Ges. 34: 740. 1916. TYPE: British Guiana [Guyana]. Rio Branco, Oct., *M. Rob. Schomburgk ser. I, 877* (lectotype, designated here, G-8918!; isolectotypes, G-8902!, K!, P [barcode] P00468593!).

Nomenclatural note. Two syntypes were cited in the protologue, *Rob. Schomburgk ser. I, 877* and *Ayres s.n.* The collection *Ayres s.n.* was not located during this study. The *Schomburgk ser. I, 877* collection matches the original description and is represented by several duplicates, and is here designated as the type; the specimen at G is selected as the lectotype because it has the best material.

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in

Venezuela (Amazonas, Bolívar), Guyana, and Brazil (Amazonas, Roraima).

24. Anemopaegma karstenii Bureau & K. Schum., Fl. Bras. 8(2): 130. 1896, as "Karstenii." TYPE: Venezuela. Carabobo: close to Puerto Caballo, s.d., *H. Karsten s.n.* (presumed holotype, B†).

Nomenclatural note. The holotype specimen is presumed to have been at B and now destroyed; no specimens of this species collected by Karsten were found at P. A broad search of other herbaria, including W, is currently being conducted for Karsten material of this species so the typification can be clarified (Firetti-Leggieri & Lohmann, in prep.).

Habitat and distribution. This species is found in evergreen lowland to montane vegetation (Gentry, 1997) in Colombia (Antioquia, Caquetá, Magdalena, Norte de Santander, Santander, Tolima, Vichada), Venezuela (Amazonas, Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Falcón Lara, Mérida, Miranda, Monagas, Portuguesa, Sucre, Táchira, Yaracuy, Zulia), Trinidad and Tobago, Guyana, and northern Brazil (Roraima).

25. Anemopaegma laeve DC., in A. DC., Prodr. 9: 189. 1845. TYPE: Brazil. Bahia: Jacobina, Marais de Japira, Vila da Barra, 1840, *J. S. Blanchet 3102* (holotype, G-DC!, G-DC as photo F neg. 7663 at MO-1692840!; isotypes, G-8920!, G-14117!, K!, P [barcode] P00468584!, P as photocopy at MO-2294580!).

Habitat and distribution. This species is found in dry caatinga and carrasco vegetation in eastern Brazil (Bahia, Ceará, Maranhão, Minas Gerais, Paraíba, Pernambuco, Piauí).

26. Anemopaegma longidens Mart. ex DC., in A. DC., Prodr. 9: 190. 1845. *Pseudopaegma longidens* (Mart. ex DC.) Urb., Ber. Deutsch. Bot. Ges. 34: 740. 1916. TYPE: Brazil. Pará: Rio Amazonas, s.d., *C. F. P. von Martius s.n.* (holotype, M-86313!, M as photo F neg. 20454 at MO-1692841!; isotype, G-DC!).

Habitat and distribution. This species is found in humid vegetation in French Guiana and Brazil (Amazonas, Goiás, Mato Grosso, Pará, Tocantins).

27. Anemopaegma longipetiolatum Sprague, Bull. Herb. Boissier, sér. 2, 5: 82. 1905. TYPE: Paraguay. Rio Apa, Nov. 1901–1902, *E. Hassler 7949* (holotype, G-14113!, G-DC as photo F neg. 26182 at MO-1185280! and MO-1692842!; isotypes, K!, MO-2187734!, MO-1573950!, NY-313068!, NY-313069!, P [barcode] P00468588!, P [barcode] P00468589!, P [barcode] P00468590!, US-2055320 image!).

Habitat and distribution. This species is found in dry forest vegetation in eastern Bolivia, Paraguay, and Brazil (Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará).

28. Anemopaegma mirabile (Sandwith) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 67. 1976. *Pseudopaegma mirabile* Sandwith, Kew Bull. 8(4): 474. 1953 [1954]. TYPE: Brazil. Piauí: banks of Gurgueia, Aug. 1839, *G. Gardner 2679* (holotype, K!; isotype, BM!).

Habitat and distribution. This species is found in dry forest vegetation in northern Brazil (Maranhão, Piauí).

29. Anemopaegma oligoneuron (Sprague & Sandwith) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 67, fig. 6. 1976. *Pseudopaegma oligoneuron* Sprague & Sandwith, Bull. Misc. Inform. Kew 1932: 88. 1932. TYPE: British Guiana [Guyana]. Upper Demerara River, Sep. 1887, *G. S. Jenman 4070* (holotype, K!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Caquetá, Meta, Vichada), Venezuela (Amazonas, Bolívar), Guyana, French Guiana, Ecuador, Peru (Loreto), and Brazil (Acre, Amazonas, Maranhão, Pará).

30. Anemopaegma orbiculatum (Jacq.) A. DC., Prodr. 9: 190. 1845. *Bignonia orbiculata* Jacq., Enum. Syst. Pl. 25. 1760. *Jacaranda orbiculata* (Jacq.) Spreng., Syst. Veg. 2: 834. 1825. *Platolaria flavescens* Raf., Sylva Tellur. 78. 1838, nom. illeg. superfl. *Peltospermum orbiculatum* (Jacq.) DC. ex Meisn., Pl. Vasc. Gen. 208. 1840. TYPE: Colombia. Magdalena: Cartagena, Sep.–Oct., *N. J. Jacquin s.n.* (holotype, W!, W as photo F neg. 32845 image!).

Habitat and distribution. This species is found in evergreen forest vegetation in Mexico (Chiapas), El Salvador, Nicaragua, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Chocó, Magdalena, Santander, Sucre, Tolima), and western Venezuela (Zulia).

31. Anemopaegma pabstii A. H. Gentry, Phytologia 46(4): 201. 1980. TYPE: Brazil. Bahia: BR-4, Km. 968, 16 Jan. 1965, *E. Pereira 9482 & G. Pabst 8371* (holotype, HB not seen; isotype, MO-2692230!).

Habitat and distribution. This species is found in cerrado vegetation in east-central Brazil (Bahia, Ceará, Goiás, Maranhão, Minas Gerais, Pará, Piauí, Tocantins).

32. Anemopaegma pachyphyllum Bureau & K. Schum., Fl. Bras. 8(2): 126. 1896. TYPE: Brazil. São Paulo, betw. São José dos Barreiros & Formosa, 10 July 1849, *A. Glaziou 11592* (holotype, P!, P as photocopy at MO-2294579!; isotype, C not seen, C as photo F neg. 22140 at MO-1692844!).

Habitat and distribution. This species is found in cerrado vegetation in central to southeastern Brazil (Bahia, Goiás, Maranhão, Pará, Piauí, São Paulo, Tocantins).

33. Anemopaegma paraense Bureau & K. Schum., Fl. Bras. 8(2): 131. 1896. TYPE: Brazil: Pará, close to Santarém, Mar. 1850, *R. Spruce 718* (lectotype, designated here, G-8919!; isolectotypes, G-14119!, G [unnumbered, 2 sheets]!, M-86314!, M-86314 as photo F neg. 20455 at MO-1692845!).

Nomenclatural note. Three syntype collections were cited in the protologue, *Martius s.n.*, *Poeppig 2896*, and *Spruce 718*. The collection *Poeppig 2896* was apparently deposited at B and later destroyed, and no duplicates have yet been located. The specimens collected by Martius were seen at M (M-86315!, M-83316!), and several duplicates of the Spruce collection were located. Spruce's collection includes the highest number of duplicates and the best quality material, and is chosen as the type; the best specimen of this set was selected as the lectotype.

Habitat and distribution. This species is known from swampy and riverside forest vegetation (Gentry, 1997) in Colombia (Amazonas, Vaupés), Venezuela (Bolívar, Delta Amacuro), Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Loreto, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Pará).

34. Anemopaegma parkeri Sprague, Bull. Herb. Boissier, sér. 2, 6: 375. 1906. TYPE: British Guiana [Guyana]. Demerara River, s.d., *W. Parker s.n.* (lectotype, designated here, K!).

Nomenclatural note. Three syntypes were listed by Sprague in the protologue: *Went 128*, *Went 377*, and *Parker s.n.* Only the Parker specimen was located at K where he worked, and this is here designated as the lectotype.

Habitat and distribution. This species is found in lowland to montane evergreen forest vegetation (Gentry, 1997) in Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Bolivia, and Brazil (Amazonas, Ceará, Maranhão, Pará, Paraíba, Piauí, Rondônia, Roraima).

35. Anemopaegma patelliforme A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 69. 1976. TYPE: Venezuela. Amazonas: Mavacá, Alto Orinoco, Yanomami Indians, Jan. 1970, *L. Aristeguieta & J. Lizot 7374* (holotype, VEN not seen, VEN as photocopy at MO-2251981!).

Habitat and distribution. This species is found in wet forest vegetation, often along streams (Gentry, 1997), in Venezuela (Amazonas, Bolívar), Bolivia, and Brazil (Mato Grosso).

36. Anemopaegma prostratum DC., in A. DC., Prodr. 9: 189. 1845. TYPE: Brazil. São Paulo: São José, Nov. 1835, *P. W. Lund 787* (lectotype, G-DC!, G-DC as photo F neg. 7662 at MO-1692747!; isolectotype, BR-880401!).

Nomenclatural note. De Candolle cited two collections in the protologue, *Lund s.n.* and *Guillemin s.n.*; the Lund specimen has a collection number on its label, and is here chosen as the lectotype.

Habitat and distribution. This species is found in seasonal and Altantic forest vegetation in Bolivia and Brazil (Bahia, Espírito Santo, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo).

37. Anemopaegma puberulum (Seibert) Miranda, Anales Inst. Biol. Nac. México 24(1): 93. 1953. *Chodanthus puberulus* Seibert, Publ. Carnegie Inst. Wash. 522: 425, tab. 7. 1940. TYPE: Mexico. Chiapas: s. loc., 17 May 1904, *E. A. Goldman 999* (holotype, US-470794 image!).

Habitat and distribution. This species is found in wet to seasonal forest vegetation in Mexico (Chiapas, Oaxaca, Veracruz), Guatemala, El Salvador, Honduras, Costa Rica, Panama, western Colombia (Cauca, Valle del Cauca), western Ecuador, and northwestern Peru (Piura, Tumbes).

38. Anemopaegma robustum Bureau & K. Schum., Fl. Bras. 8(2): 123. 1896. TYPE: British Guiana [Guyana]. River Essequibo, s.d., *Rich. H. Schomburgk 355* (presumed holotype, B†).

Nomenclatural note. No type material of this name has yet been located. An ongoing taxonomic

revision of this genus will clarify the typification of this species (Firetti-Leggieri & Lohmann, in prep.).

Habitat and distribution. This species is found in humid lowland forest vegetation in Venezuela (Amazonas, Bolívar), Guyana, French Guiana, Brazil (Amazonas), and possibly northeastern Peru (Loreto; Gentry, 1997).

39. Anemopaegma rugosum (Schltdl.) Sprague, Bull. Misc. Inform. Kew 1931: 233. 1931. *Bignonia rugosa* Schltdl., Linnaea 26: 856. 1854. TYPE: Venezuela. Miranda: Chacao, s.d., *Wagener 437* (holotype, HAL not seen).

Habitat and distribution. This species is found in evergreen forest vegetation in the Cordillera de la Costa in northern Venezuela (Aragua, Distrito Federal, Miranda).

40. Anemopaegma salicifolium (Kunth) Sandwith, Lilloa 3: 459. 1938. *Bignonia salicifolia* Kunth, Nov. Gen. Sp. 3: 133. 1818 [1819]. TYPE: Venezuela. River Orinoco, Apr., *F. W. H. A. von Humboldt & A. J. A. Bonpland 5027* (holotype, P-Bonpl. [barcode] P00468586!, P-Bonpl. as photo F neg. 39414 at MO-1692915!).

Habitat and distribution. This species is found in seasonally flooded forest vegetation in the Orinoco River basin of Venezuela (Amazonas, Bolívar) and presumably eastern Colombia (Gentry, 1997), and perhaps is also found in Brazil (Amazonas).

41. Anemopaegma santaritense A. H. Gentry, Ann. Missouri Bot. Gard. 58(1): 93, fig. 2. 1971, as "santa-ritensis." TYPE: Panama. Colón: SE of Santa Rita Ridge, 14 Feb. 1969, *A. H. Gentry 454* (holotype, MO-2018469!; isotypes, MO-2017611!, MO-2018468!, WIS not seen).

Habitat and distribution. This species is found in premontane forest vegetation in Costa Rica, Panama, and Colombia (Chocó, Cundinamarca, Santander).

42. Anemopaegma scabriusculum Mart. ex DC., in A. DC., Prodr. 9: 188. 1845. TYPE: Brazil. Minas Gerais: close to Serra de Santo Antônio & Contendas, July, *C. F. P. von Martius 501* (holotype, G-DC!; isotypes, M-86317!, M as photo F neg. 20456 at MO-1692749!, P [barcode] P00468587!).

Habitat and distribution. This species is found in cerrado and dry campo rupestre vegetation in central to eastern Brazil (Bahia, Goiás, Maranhão, Minas Gerais, Pará, Piauí, Tocantins).

43. Anemopaegma setilobum A. H. Gentry, Phytologia 46(4): 203. 1980. TYPE: Brazil. Espírito Santo: betw. Linhares & São Mateus, 22 Feb. 1965, *A. P. Duarte 8861* (holotype, RB-126214!; isotypes, HB not seen, MO-2193067!, MO-2698298!).

Habitat and distribution. This species is found in wet forest vegetation in central and eastern Brazil (Bahia, Espírito Santo, Maranhão, Minas Gerais, Pará, Piauí).

44. Anemopaegma velutinum Mart. ex DC., in A. DC., Prodr. 9: 189. 1845. TYPE: Brazil. Minas Gerais: Serro Frio, Aug. 1818, *C. F. P. von Martius s.n.* (lectotype, designated here, M-86319!; isolectotypes, BR-839801!, M-86320!).

Nomenclatural note. De Candolle did not cite a collection number in the protologue for this species, but reported that a specimen was seen in Martius's herbarium and that the species was known from Espírito Santo, Bahia, and Minas Gerais. Hence, a Martius collection of this species from Minas Gerais with duplicates in both M and BR is here selected as the type; there are two specimens at M, one with flowers and one with fruits, and the M specimen with flowers is here selected as the lectotype. A composite photo (F neg. 20457 at MO-1692754!) shows parts of both of the M sheets.

Habitat and distribution. This species is found in scrub vegetation on rocky outcrops in eastern Brazil (Bahia, Minas Gerais, Piauí).

45. Anemopaegma villosum A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 70. 1976. TYPE: Venezuela. Portuguesa: 5 km NE of Agua Blanca, 22 km NE of Acarigua, 190 m, 24 Aug. 1966, *J. A. Steyermark 96455* (holotype, VEN not seen, VEN as photocopy at MO-2300555!; isotypes, NY-313077!, US-2481599 image!).

Habitat and distribution. This species is found in forest vegetation, generally on calcareous soils, in northern Venezuela (Distrito Federal, Portuguesa).

IV. Bignonia L., Sp. Pl. 622. 1753. TYPE: *Bignonia capreolata* L., typ. cons.

Cydista Miers, Proc. Roy. Hort. Soc. London. 3: 191. 1863, syn. nov. TYPE: *Cydista aequinoctialis* (L.) Miers [≡ *Bignonia aequinoctialis* L.].

Anisostichus Bureau, Monogr. Bignon. 43. 1863. nom. superfl. illeg. TYPE: *Anisostichus capreolata* (L.) Bureau [≡ *Bignonia capreolata* L.].

Clytostoma Miers ex Bureau, Adansonia 8: 353. 1868, syn. nov. TYPE: *Clytostoma callistegioides* (Cham.) Bureau ex Griseb. [≡ *Bignonia callistegioides* Cham.].

Phryganocydia Mart. ex Bureau, Bull. Soc. Bot. France 19: 18. 1872, syn. nov. *Phrygiobureaua* Kuntze, in Post. & Kuntze, Lex. Gen. Phan. 433. 1903 [1904], nom. superfl. illeg. TYPE: *Phryganocydia corymbosa* (Vent.) Bureau ex K. Schum. [≡ *Bignonia corymbosa* (Vent.) L. G. Lohmann.].

Levya Bureau ex Baill., Hist. Pl. 10: 28. 1888. TYPE: *Levya nicaraguensis* Bureau ex Baill. [= *Bignonia aequinoctialis* L.].

Mussatia Bureau ex Baill., Hist. Pl. 10: 32. 1888, syn. nov. TYPE: *Mussatia prieurii* (DC.) Bureau ex K. Schum. [≡ *Bignonia prieurii* DC.].

Osmhydrophora Barb. Rodr., Vellosia, ed. 2, 1: 49. 1891, *Osmohydrophora*, orth. var. TYPE: *Osmhydrophora nocturna* Barb. Rodr. [≡ *Bignonia nocturna* (Barb. Rodr.) L. G. Lohmann.].

Macranthisiphon Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 219. 1894, syn. nov. TYPE: *Macranthisiphon longiflorus* (Cav.) K. Schum. [≡ *Bignonia longiflora* Cav.].

Roentgenia Urb., Ber. Deutsch. Bot. Ges. 34: 747. 1916, syn. nov. TYPE: *Roentgenia bracteomana* (K. Schum.) Urb. [≡ *Bignonia bracteomana* (K. Schum.) L. G. Lohmann].

Potamoganos Sandwith, Receuil Trav. Bot. Néerl. 34: 220. 1937, syn. nov. TYPE: *Potamoganos microcalyx* (G. Mey.) Sandwith [≡ *Bignonia microcalyx* G. Mey.].

Saritaea Dugand, Caldasia 3: 262. 1945, syn. nov. TYPE: *Saritaea magnifica* (W. Bull) Dugand (≡ *Bignonia magnifica* W. Bull).

Clytostomanthus Pichon, Bull. Soc. Bot. France 92: 224. 1946. TYPE: *Clytostomanthus decorus* (S. Moore) Pichon [≡ *Bignonia decora* (S. Moore) L. G. Lohmann].

Micropaegma Pichon, Bull. Soc. Bot. France 92: 225. 1946. TYPE: *Micropaegma brachycalyx* (Bureau & K. Schum) Pichon [= *Bignonia prieurii* DC.].

Lianas or shrubs, without dimorphic juvenile growth, without strong odor; stems with phloem wedges in multiples of 4 in cross-section, pith solid; branchlets cylindrical, irregularly angled, or tetragonal, glabrous (puberulous), without lenticels or with sparsely distributed lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds foliaceous and bromeliad-like (minute and triangular), with or without glands. Leaves 2-foliolate, terminal leaflet often replaced by a simple (minutely trifid or multifid) tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous to coriaceous, with glands grouped in axils of veins or sparsely distributed on lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a cyme, thyrse, fascicle, or raceme. Flowers zygomorphic, pentamerous; calyx cupular or tubular, shortly 5-lobed, 5-apiculate, or bilabiate, coriaceous, glabrous, puberulous, or villose externally, with or without glands near margins; corolla magenta (yellow, white, red), with or without nectar guides, tubular or infundibuliform and frequently dorso-ventrally flattened, straight in tube, membranaceous, glabrous to villose externally, without (with) glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included (exserted), anthers glabrous, thecae straight, pollen in monads, inaperturate, colpate or porate, with exine reticulate or complex; ovary sessile, smooth or papillate and glabrous or lepidote externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular or absent. Capsules linear (elliptic), flattened or inflated, straight, woody or coriaceous, with valves 2, glabrous, without lenticels, without glands, without wings, smooth, echinate, or tuberculate, with calyx caducous; seeds winged, with body smooth and glabrous, wings opaque, linear or rounded. Figures 10 and 11.

Number of species, distribution, and habitat. *Bignonia* includes 28 species found in wet to dry tropical forest and warm temperate forest vegetation from the southern U.S.A. to Argentina.

Bignonia is circumscribed much more broadly here than by recent authors, based on both morphological and molecular characters. It here includes *Cydista*, *Clytostoma*, *Macranthisiphon*, *Mussatia*, *Phryganocydia*, *Potamoganos*, *Roentgenia*, and *Saritaea*. In this wider circumscription *Bignonia* is characterized by stems in cross-section with eight phloem wedges that are often cylindrical and tetragonal within the same individual, consistently 2-foliolate leaves (e.g., Fig. 10A) with dense gland fields in the vein axils of the leaflets, simple or lepidote trichomes, simple or sometimes very shortly 3-parted tendrils, prophylls of the axillary buds that are foliaceous (Fig. 11O, S), bromeliad-like, or both (Fig. 11A, F, J), a single series of ovules on each placenta, reticulate pollen exine, and opaque seed wings.

The affinities among *Cydista*, *Clytostoma*, *Mussatia*, *Phryganocydia*, *Potamoganos*, and *Roentgoenia* have been hypothesized before (Gentry, 1973a; Hauk, 1997, 2002), based on a suite of shared morphological characters and especially the unusual mimetic pollination strategy, with the corollas dorso-ventrally flattened and displaying prominent nectar guides, although no nectar disk is present (Fig. 12) so the pollinators are deceived. *Mussatia* and *Clytostoma* in particular are similar (see Fig. 10B, D), and were separated based mainly on their fruits, elliptic and echinate in *Clytostoma* versus linear and smooth to tuberculate in *Mussatia* (Figs. 11C, H, 12). These were separated, even though Gentry himself noted (1973a: 241) that "[t]he fact that some species with

very different fruit morphologies are very closely related shows the inadvisability of arbitrarily segregating genera entirely on the basis of such characters." On the other hand, the relationship among these genera and *Bignonia*, *Saritaea*, *Macranthisiphon*, and *Tanaecium nocturnum* (Fig. 10C) has not been noted before. *Bignonia* in recent decades has been separated as a monotypic genus based on its combination of multifid tendrils, fasciculate inflorescences, and North American distribution (Fig. 12). *Saritaea* and *Macranthisiphon* were separated based on combinations of characters but considered related to each other based on their shared porate pollen with a complex exine ornamentation pattern, a form unique in the tribe Bignonieae. The hawkmoth-pollinated species *T. nocturnum* (Fig. 11C), on the other hand, was thought to be related to other hawkmoth-pollinated species of *Tanaecium*, even though *T. nocturnum* differs completely from the other species classified in *Tanaecium* in its eight phloem wedges and uniseriate ovules. The phylogenetic hypothesis of Bignonieae (Lohmann, 2006) indicates that, once again in this tribe, many flower and fruit characters are variable, while other features such as stem anatomy and ovule arrangement are good indicators of systematic relationships.

Within this *Bignonia* clade (Fig. 12) there are no clear patterns of characters nor well-supported subgroups, so systematically meaningful units cannot be separated. This clade as a whole is well characterized and therefore here circumscribed as a single genus, which takes the name *Bignonia*. *Macranthisiphon* was originally included here solely based on morphological affinities, but recent molecular phylogenetic studies corroborate its placement in the genus (Zuntini & Lohmann, in prep.).

1. Bignonia aequinoctialis L., Sp. Pl. 623. 1753. *Cydista aequinoctialis* (L.) Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. TYPE: tab. 58, Burman, Pl. Amer., 1756 (lectotype, designated by Gentry [1977: 57]).

Habitat and distribution. This species is commonly found in evergreen lowland to montane forest and disturbed vegetation (Gentry, 1997) in Mexico (Chiapas, Colima, Guerrero, Jalisco, Nayarit, Oaxaca, Sinaloa, Tabasco, Veracruz, Yucatán), the Antilles (Antigua, Barbados, Cuba, Dominica, Dominican Republic, Grenada, the Grenadines, Guadeloupe, Haiti, Martinique, Puerto Rico, St. Lucia, St. Vincent, Virgin Islands), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Atlántico, Bolívar, Boyacá, Caquetá, César, Chocó, Córdoba, Cundinamarca, Guaviare, Magdalena, Meta, Nariño, Norte de Santander, Santander, Sucre, Tolima, Valle del Cauca, Vaupés, Vichada), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Falcón, Lara, Mérida, Miranda, Monagas, Sucre, Táchira, Trujillo, Zulia), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Junín, Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Rondônia, Roraima).

2. Bignonia binata Thunb., Pl. Bras. 3: 35. 1821. *Clytostoma binatum* (Thunb.) Sandwith, Receuil Trav. Bot. Néerl. 34: 231. 1937. TYPE: Brazil. s. loc., s.d., *G. W. Freyreis s.n.* (holotype, UPS-14225!).

Habitat and distribution. This species is found in swampy, usually riverside lowland forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Jalisco, Oaxaca, Quintana Roo, Tabasco, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Caquetá, Chocó, Meta, Nariño, Putumayo, Santander, Sucre, Valle del Cauca, Vaupés, Vichada), Venezuela (Amazonas, Anzoátegui, Apure, Bolívar, Delta Amacuro, Guárico, Sucre, Táchira, Zulia), Guyana, Suriname, French Guiana, Ecuador, Peru (Huánuco, Loreto, Madre de Dios, Puno, San Martín, Tumbes, Ucayali), Bolivia, Paraguay, Brazil (Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraiba, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo), and Argentina (Chaco, Corrientes, Misiones, Salta).

3. Bignonia bracteomana (K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Cydista bracteomana* K. Schum., in Sprague, Verh. Bot. Vereins Prov. Brandenburg 50: 121. 1908 [1909]. *Roentgenia bracteomana* (K. Schum.) Urb., Ber. Deutsch. Bot. Ges. 34: 748. 1916. *Bignonia bracteomana* (K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 763. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Victoria, Rio Juruá, May 1901, *E. Ule 5497* (holotype, B†; isotypes, HBG not seen, L not seen, MG not seen).

Nomenclatural note. The holotype specimen has been destroyed, and several duplicates have been cited in the literature but not seen in this study. Additional material may also exist, therefore more work is necessary before the typification of this

species can be clarified. Ongoing monographic studies of *Bignonia* are addressing this problem (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is found in lowland wet forest vegetation in Colombia (Caquetá, Putumayo), Ecuador, Peru (Amazonas, Loreto, Madre de Dios, Puno, San Martín, Ucayali), Bolivia, and Brazil (Amazonas, Maranhão).

4. **Bignonia callistegioides** Cham., Linnaea 7: 712. 1832 [1833]. *Cuspidaria callistegioides* (Cham.) DC., in A. DC., Prodr. 9: 178. 1845. *Clytostoma callistegioides* (Cham.) Bureau ex Griseb., Symb. Fl. Argent. 257. 1879, as "*calystegioides*." *Pithecoctenium callistegioides* (Cham.) Niederl., Bol. Mens. Mus. Prod. Argent. 3(31): 320. 1890, as "*calystegioides*." TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, G-DC!, NY-313137!).

Habitat and distribution. This species is found in dry forest vegetation in Bolivia, Paraguay, Brazil (Rio Grande do Sul), Uruguay, and Argentina (Buenos Aires, Corrientes, Entre Ríos, Jujuy, Misiones, Salta), and also is widely cultivated.

5. **Bignonia campanulata** Cham., Linnaea 7: 711. 1832 [1833]. *Cuspidaria campanulata* (Cham.) DC., Prodr. 9: 179. 1845. *Clytostoma campanulatum* (Cham.) Bureau & K. Schum., Fl. Bras. 8(2): 148. 1896. TYPE: Brazil. s. loc., s.d., *F. Sellow 182* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18434 at MO-1185443!, BR-880329!, NY-313138!).

Habitat and distribution. This species is found in humid and Atlantic forest vegetation in Peru (Madre de Dios), northern Bolivia, and Brazil (Bahia, Minas Gerais, Paraíba, Rio de Janeiro, São Paulo).

6. **Bignonia capreolata** L., Sp. Pl. 2: 624. 1753. *Doxantha capreolata* (L.) Miers, Proc. Roy. Hort. Soc. London 3: 190. 1863. *Anisostichus capreolata* (L.) Bureau, Monogr. Bignon. 43. 1864. TYPE: Herb. Clifford: 317, Bignonia no. 2 excluding open flower (lectotype, designated by Reveal [1993: 24]).

Habitat and distribution. This species is found in warm temperate forest and disturbed vegetation in the southeastern United States (Alabama, Arkansas, Florida, Georgia, Illinois, Kentucky, Louisiana, Maryland, Mississippi, Missouri, North Carolina, South Carolina, Tennessee, Texas, Virginia, West Virginia).

7. **Bignonia convolvuloides** (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Clytostoma convolvuloides* Bureau & K. Schum., Fl. Bras. 8(2): 154. 1896. *Bignonia convolvuloides* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 763. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Jacobina, June 1844, *J. S. Blanchet 3849* (lectotype, designated here, P [barcode] P00481528!; isolectotypes, BR-880355!. G-9449!, G-9450!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Sellow 734* and *Blanchet 3849*. The *Sellow 734* material presumably deposited at B has been destroyed and duplicate material has not been located, hence the collection *Blanchet 3849* is here designated as the type with the sheet at P chosen as the lectotype because it is in good condition and could have been studied by Bureau.

Habitat and distribution. This species is found in dry forest vegetation in Bolivia, Paraguay, and Brazil (Bahia, Mato Grosso, Minas Gerais, Pernambuco).

8. **Bignonia corymbosa** (Vent.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Spathodea corymbosa* Vent., Mem. Cl. Sci. Math. Inst. Natl. France 8: 19. 1807. *Macfadyena corymbosa* (Vent.) Griseb., Bonplandia (Hannover) 6: 10. 1858. *Phryganocydia corymbosa* (Vent.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 224. 1894. *Phrygiobureaua corymbosa* (Vent.) Kuntze, Lex. Gen. Phan. 433. 1903 [1904]. TYPE: Trinidad. s. loc., s.d., *A. Riedlé s.n.* (holotype, P [barcode] P00481551!).

Habitat and distribution. This species is found frequently in semideciduous to evergreen forest and disturbed vegetation (Gentry, 1997) in the Lesser Antilles (Grenada, Martinique, St. Vincent, Virgin Islands), Costa Rica, Panama, Colombia (Antioquia, Atlántico, Bolívar, Boyacá, Caldas, Caquetá, César, Chocó, Córdoba, La Guajira, Magdalena, Meta, Nariño, Norte de Santander, Santander, Sucre, Vaupés, Vichada), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Federal, Falcón, Guárico, Lara, Miranda, Monagas, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia), Trinidad and Tobago, Guyana, French Guiana, Ecuador, Peru (Loreto), Bolivia, and Brazil (Acre, Alagoas, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Pernambuco, Rio de Janeiro, Rondônia).

9. Bignonia costata (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Clytostoma costatum* Bureau & K. Schum., Fl. Bras. 8(2): 150. 1896. TYPE: Brazil. Rio de Janeiro: Rio Jaú, close to Maxambamba, 19 Oct. 1876, *A. Glaziou 8813* (lectotype, designated here, P [barcode] P00481532!; isolectotypes, BR-880497!, BR-880530!, C not seen, C as photo F neg. 322131 at MO-1692953!, G-9448!, K [barcode] K000449464!, K [barcode] K000449465!, NY-328759!, NY as photocopy at MO-2927253!, P [barcode] P00481531!, P [barcode] P00481533!).

Nomenclatural note. Four syntypes were cited in the original description of *Clytostoma costata*, *Glaziou 849*, *Glaziou 2108*, *Glaziou 6815*, and *Glaziou 8813*. The collection *Glaziou 8813* has the best material, the highest number of duplicates, and the widest distribution and is chosen here as the type. The sheet P [barcode] P00481532 is designated as the lectotype because it has ample material with the most typical leaf form.

Habitat and distribution. This species is found in wet forest vegetation in southeastern Brazil (Rio de Janeiro).

10. Bignonia cuneata (Dugand) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Clytostoma cuneatum* Dugand, Caldasia 3(13): 259. 1945. TYPE: Colombia. Atlántico: betw. Palmar de Varela & Ponedora, finca El Paraiso, 2–4 Aug. 1943, *A. Dugand & R. Jaramillo 3457* (lectotype, designated here, COL-14544 image!; isolectotype, COL-14545 image!).

Nomenclatural note. Four different collections were cited in the protologue of *Clytostoma cuneatum*, with only one explicitly designated as the type and the other three called co-types. The term co-type was often used contemporaneously to designate isotypes and these other collections have been interpreted as such in sched. However, in this case Dugand stated that the co-types were used in the preparation of the description in addition to the type, and thus these are clearly paratypes in today's terminology. Dugand did not list or distinguish duplicates of the type collection in this protologue, but two specimens of this are deposited at COL; the specimen with more, better material is here designated as the lectotype.

Habitat and distribution. This species is found in seasonal forest vegetation in northern Colombia (Atlántico, Bolívar) and northwestern Venezuela (Falcón, Miranda).

11. Bignonia decora (S. Moore) L. G. Lohmann, comb. nov. Basionym: *Anemopaegma decorum* S. Moore, Trans. Linn. Soc. London, ser. 2, 4: 421. 1895. *Clytostoma decorum* (S. Moore) Bureau & K. Schum., Fl. Bras. 8(2): 151. 1896. *Arrabidaea decora* (S. Moore) Hassl., Repert. Spec. Nov. Regni Veg. 9: 49. 1910. *Clytostomanthus decorus* (S. Moore) Pichon, Bull. Soc. Bot. France 92: 224. 1945. *Cydista decora* (S. Moore) A. H. Gentry, Selbyana 2: 42. 1977. *Bignonia decora* (S. Moore) L. G. Lohmann, Cat. Pl. Vasc. Cono Sur 2: 1595. 2008, nom. nud. invalid. *Bignonia decora* (S. Moore) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 763, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Corumbá, Jan. 1891–1892, *S. Moore "980" [950]* (holotype, BM!; isotype, NY-313062!).

Nomenclatural note. Moore (1895) cited the same type specimen number, 980, for *Adenocalymma croceum* S. Moore and *Anemopaegma decorum*, but these are distinct species and their respective type specimens represent the corresponding species. The holotype specimen of *Adenocalymma croceum* at BM does have two labels with two different collection numbers, 950 and 980, but this specimen is currently databased at BM under the number 950 and that is here assumed to be the correct number.

Habitat and distribution. This species is found in dry forest vegetation in western Ecuador, Bolivia, Paraguay, and Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná).

12. Bignonia diversifolia Kunth, Nov. Gen Sp. Pl. 3: 133. 1818 [1819]. *Cydista diversifolia* (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. *Pleonotoma diversifolia* (Kunth) Bureau & K. Schum., Fl. Bras 8(2): 274. 1897. TYPE: Mexico. Campeche: s. loc., s.d., *A. J. A. Bonpland s.n.* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39412 at MO-1692918!).

Habitat and distribution. This species is found frequently in wet to dry vegetation in Mexico (Campeche, Chiapas, Guerrero, Jalisco, Michoacán, Oaxaca, Quintana Roo, Tabasco, Yucatán), the Greater Antilles (Cuba), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Atlántico, Bolívar, Boyacá, César, Cundinamarca, Huila, La Guajira, Magdalena, Norte de Santander, Santander, Sucre, Tolima, Valle del Cauca), Venezuela (Anzoátegui, Aragua, Carabobo, Coejedes, Distrito Federal, Falcón, Guárico, Lara, Miranda, Portuguesa, Táchira, Trujillo, Yaracuy,

Zulia), and Brazil (Goiás, Maranhão, Mato Grosso, Tocantins).

13. Bignonia hyacinthina (Standl.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Tynanthus hyacinthinus* Standl., Publ. Carnegie Inst. Wash. 461(4): 87. 1935. *Mussatia hyacinthina* (Standl.) Sandwith, Recueil Trav. Bot. Néerl 34: 218. 1937. TYPE: British Honduras [Belize]. Jacinto Creek, 60 ft., 28 Apr. 1934, *W. A. Schipp S-661* (holotype, F-733483 image!, F-733483 as unnumbered photo at MO-1183674!; isotypes, G!, K!, NY-328980!).

Habitat and distribution. This species is found in semideciduous to evergreen lowland forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Guerrero, Oaxaca, Puebla, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Chocó, La Guajira, Meta, Valle del Cauca), Venezuela (Amazonas, Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Federal, Mérida, Miranda, Monagas, Táchira, Yaracuy, Zulia), Guyana, Ecuador, Peru (Loreto, Madre de Dios, Pasco, Puno, San Martín), Bolivia, and Brazil (Acre, Pará, Roraima).

14. Bignonia lilacina (A. H. Gentry) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Cydista lilacina* A. H. Gentry, Mem. New York Bot. Gard. 29: 277, figs. 124B, 125. 1978. TYPE: Venezuela. Bolívar: Tumeremo to Anacoco (N side of Cuyuni River), 56–57 km from Guyana frontier at Anacoco, 140–200 m alt., 18 Mar. 1974, *A. H. Gentry, G. Morillo & B. de Morillo 10673* (holotype, MO-2198604!; isotypes, MO-2198605!, VEN not seen).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Bolívar), Venezuela (Amazonas, Barinas, Bolívar, Delta Amacuro, Sucre), Suriname, French Guiana, Ecuador, Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Maranhão, Mato Grosso, Minas Gerais, Pará, Rondônia, Roraima).

15. Bignonia longiflora Cav., Icon. 6: 58, tab. 581. 1801. *Pyrostegia longiflora* (Cav.) Miers, Proc. Roy. Hort. Soc. London 3: 188. 1863. *Macranthisiphon longiflorus* (Cav.) K. Schum., Nat. Pflanzenfam. 4(3b): 219. 1894. TYPE: Ecuador. Guayaquil, s.d., *L. Nee s.n.* (lectotype, designated here, MA-652465!, MA-652465 as photo F neg. 29231 at MO-1692897!; isolectotype, MA-475442!).

Nomenclatural note. Cavanilles's material is deposited in Madrid (Stafleu & Cowan, 1976), and the specimen found there with the best material is here selected as the lectotype.

Habitat and distribution. This species is found in seasonal vegetation in western Ecuador (El Oro, Guayas, Loja, Manabí) and northwestern Peru (Piura, Tumbes).

16. Bignonia magnifica W. Bull, Gard. Chron., n. s. 12: 72, fig. 9. 1879. *Arrabidaea magnifica* (W. Bull) Sprague ex Steenis, Receuil Trav. Bot. Néerl. 24: 830. 1927. *Saritaea magnifica* (W. Bull) Dugand, Caldasia 3: 263. 1945. TYPE: Colombia. Magdalena: Santa Marta, 1500 ft., Sep. 1898–1901, *H. H. Smith 741* (neotype, designated by Steenis [1927: 830], U not seen; isoneotypes, BM!, BR!, K [barcode] K000404058!, K [barcode] K000404059!, MO-2005575!, NY [barcode] NY00313101!, NY [barcode] NY00313102!, US-600311 image!).

Habitat and distribution. This species is found in wet forest vegetation in the Greater Antilles (Cuba, Dominican Republic, Jamaica), Panama, Colombia (Atlántico, César, Magdalena, Norte de Santander, Risaralda, Santander, Valle del Cauca), Venezuela (Distrito Federal, Guárico, Miranda), and Ecuador, and is cultivated in tropical regions worldwide.

17. Bignonia microcalyx G. Mey., Prim. Fl. Esseq. 211. 1818. *Anemopaegma microcalyx* (G. Mey.) Bureau & K. Schum., Fl. Bras. 8(2): 134. 1896. *Potamoganos microcalyx* (G. Mey.) Sandwith, Receuil Trav. Bot. Néerl. 34: 220. 1937. TYPE: British Guiana [Guyana]. s. loc., s.d., *G. Meyer s.n.* (holotype, GOET not seen).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Amazonas), Guyana, Suriname, and Brazil (Amapá, Amazonas, Pará).

18. Bignonia neoheterophylla L. G. Lohmann, nom. nov. Replaced name: *Cydista heterophylla* Seibert, Publ. Carnegie Inst. Wash. 522: 417. 1940, non *Bignonia heterophylla* Willd., 1800 [1801]. TYPE: Mexico. Yucatán: near Xocenpich, May–Aug 1938, *C. L. Lundell & A. A. Lundell 7350* (holotype, MICH not seen, MICH as unnumbered photo at MO-1244826!; isotypes, A not seen, F-1309020 image!, LL

[unnumbered, 2] not seen, LL as photocopies at MO-3571763! and MO-3571764!, S not seen, US-1840031 image!).

Nomenclatural note. The name *Bignonia heterophylla* has already been published for another species, and although this name is now considered a synonym of *Pachyptera kerere* (Aubl.) Sandwith, it still exists. Therefore when the name *Cydista heterophylla* is transferred to *Bignonia* it needs a new name in the latter genus, which is provided here.

Habitat and distribution. This species is found frequently in humid to usually dry vegetation in Mexico (Campeche, Chiapas, Guerrero, Jalisco, Nayarit, Oaxaca, Quintana Roo, Tabasco, Veracruz, Yucatán), the Greater Antilles (Cuba), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Colombia (Bolívar, Sucre).

19. Bignonia neouliginosa L. G. Lohmann, nom. nov. Replaced name: *Phryganocydia uliginosa* Dugand, Caldasia 4(16): 59. 1946, non *Bignonia uliginosa* Gomes, 1803. TYPE: Colombia. Atlántico: betw. Palmar de Varela & Ponedera, swamps of Río Magdalena, farm El Paraíso, 2–4 Aug. 1943, *A. Dugand & R. Jaramillo 3491* (holotype, COL-14564 image!; isotype, US-1852300 image!).

Nomenclatural note. The name *Bignonia uliginosa* has already been published for another species, and although this name is now considered a synonym of *Tabebuia cassinoides* (Lam.) DC., it still exists. Therefore when the name *Phryganocydia uliginosa* is transferred to *Bignonia* it needs a new name, which is provided here.

Habitat and distribution. This species is found in swampy forest vegetation in the Magdalena River valley of Colombia (Atlántico, Bolívar, César, Santander).

20. Bignonia nocturna (Barb. Rodr.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Osmhydrophora nocturna* Barb. Rodr., Vellosia, ed. 2, 1: 49, 3: tab. 8, 9. 1885–1888 [1891]. *Tanaecium nocturnum* (Barb. Rodr.) Bureau & K. Schum., Fl. Bras. 8(2): 185. 1896. TYPE: Brazil. Amazonas: forests of Rio Purus & secondary vegetation near Manaus, Feb., *J. Barbosa Rodrigues s.n.* (holotype, not located).

Nomenclatural note. The type of *Osmhydrophora nocturna* has not been located at RB, where the surviving material of Barbosa Rodrigues is deposited. Many of his types were at INPA, and most of those have been lost (Mori & Ferreira, 1987). Further study is needed for the typification of this species (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is found widely in wet forest vegetation in eastern Panama, Colombia (Amazonas, Antioquia, Bolívar, Chocó, Santander), Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Goiás, Mato Grosso, Pará, Rondônia).

21. Bignonia phellosperma (Hemsl.) L. G. Lohmann, comb. nov. Basionym: *Macfadyena phellosperma* Hemsl., Biol. Cent.-Amer., Bot. 2(12): 492. 1882. *Phryganocydia phellosperma* (Hemsl.) Sandwith, Bull. Misc. Inform. Kew 1940(7): 302. 1940 [1941]. TYPE: Panama. Canal Zone [Coclé]: swamps of Río Grande, June 1861, *S. Hayes 81* (holotype, K!; isotype, BM-630059!).

Habitat and distribution. This species is found in mangrove vegetation along the Pacific coast of Costa Rica, Panama, and Colombia (Chocó, Nariño).

22. Bignonia potosina (K. Schum. & Loes.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea potosina* K. Schum. & Loes., Bull. Herb. Boissier 3(12): 618. 1895. *Cydista potosina* (K. Schum. & Loes.) Loes., Repert. Spec. Nov. Regni Veg. 16: 209. 1919. TYPE: Mexico. San Luis Potosí, s.d., *G. E. Seler & C. Seler 616* (holotype, B†).

Nomenclatural note. Ongoing work will clarify the typification of this species (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is found in wet and seasonal forest vegetation in Mexico (Campeche, Chiapas, Oaxaca, Puebla, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, and northern Costa Rica.

23. Bignonia prieurii DC., in A. DC., Prodr. 9: 154. 1845, as "*prieurei.*" *Panterpa prieurii* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 196. 1863. *Mussatia prieurii* (DC.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 224. 1894. TYPE: French Guiana. s. loc., 1834, *F. R. Le Prieur 273* (holotype, G-DC!, G-DC as photo F neg. 26198 at MO-1692901!; isotypes, G-9262!, G [no #] as photo F neg. 7639 at MO-169202!, P [barcode] P00468591!, P [barcode] P00468592!).

Habitat and distribution. This species is found in evergreen lowland forest (Gentry, 1997) in Colombia (Amazonas, Caquetá, Vaupés), Venezuela (Amazonas, Bolívar), Guyana, French Guiana, Suriname, Ecuador, Peru (Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Bahia, Espírito Santo, Minas Gerais, Pará, Rondônia).

24. Bignonia pterocalyx (Sprague ex Urb.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Clytostoma pterocalyx* Sprague ex Urb., Ber. Deutsch. Bot. Ges. 34: 741. 1916. TYPE: Colombia. Magdalena: Santa Marta, 150 ft., 1898, *H. H. Smith 2401* (holotype, B†; lectotype, designated here, NY-328761!; isolectotypes, BR!, F-139139 image!, G-9663!, MO-1998976!, NY [barcode] NY00328760!, NY [barcode] NY00579039!, P [barcode] P00481526!, P [barcode] P00481527!, US-600410 image!).

Nomenclatural note. The lectotype chosen here is the specimen with the best material, which is also part of Smith's main set at NY.

Habitat and distribution. This species is found in wet forest vegetation in northern Colombia (Antioquia, Atlántico, Bolívar, César, Madgalena, Sucre) and northwestern Venezuela (Lara, Trujillo, Zulia).

25. Bignonia ramentacea (Mart. ex DC.) L. G. Lohmann, comb. nov. Basionym: *Cuspidaria ramentacea* Mart. ex DC., in A. DC., Prodr. 9: 178. 1845. *Clytostoma ramentaceum* (Mart. ex DC.) Bureau & K. Schum., Fl. Bras. 8(2): 150. 1896. *Bignonia ramentacea* (Mart. ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 763. 2010, nom. nud. invalid., as "ramantacea." TYPE: Brazil. Minas Gerais: betw. Salgado & Contendas, Aug. 1818, *C. F. P. von Martius s.n.* (holotype, M-86401!, M as photo F neg. 20459 at MO-1692937!; isotype, G-DC!).

Habitat and distribution. This species is found in dry caatinga and cerrado vegetation in eastern Brazil (Bahia, Ceará, Mato Grosso, Minas Gerais, Pernambuco).

26. Bignonia sciuripabulum (K. Schum.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008, as "*sciuripabula*." *Arrabidaea sciuripabulum* K. Schum., Nat. Pflanzenfam. 4(3b): 224. 1894. *Clytostoma sciuripabulum* (K. Schum.) Bureau & K. Schum., Fl. Bras. 8(2): 149. 1896. *Pithecoctenium sciuripabulum* (K. Schum.) Corr. Méllo, Arq. Mus. Paranaense 9: 53. 1952. TYPE: Brazil. São Paulo: Campinas, 20 Sep. 1867, *J. Correia de Méllo 22* (holotype, B†; isotypes, C not seen, C as photo F neg. 22132 at MO-1692938!, K [2] not seen, K as photocopies at MO-2904347! and MO-2904348!).

Nomenclatural note. Ongoing monographic study of *Bignonia* will clarify the typification of this species (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is commonly and widely collected in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Córdoba), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Bolívar, Carabobo, Distrito Federal, Lara, Miranda, Nueva Esparta), Guyana, Ecuador, Peru (Amazonas, Cusco, Junín, Loreto, Madre de Dios, Puno, Ucayali), Bolivia, Paraguay, Brazil (Acre, Alagoas, Amazonas, Bahia, Espírito Santo, Maranhão, Mato Grosso, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo), and Argentina (Misiones).

27. Bignonia sordida (Bureau & K. Schum.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Arrabidaea sordida* Bureau & K. Schum., Fl. Bras. 8(2): 30. 1896. *Roentgenia sordida* (Bureau & K. Schum.) Sprague & Sandwith, Bull. Misc. Inform. Kew 1932: 91. 1932. TYPE: British Guiana [Guyana]. Upper Rupununi River, s.d., *Rich. H. Schomburgk 1296* (holotype, B†).

Nomenclatural note. Ongoing monographic study of *Bignonia* will clarify the typification of this species (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Venezuela (Bolívar, Delta Amacuro), Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Goiás, Maranhão, Pará, Tocantins).

28. Bignonia uleana (Kraenzl.) L. G. Lohmann, comb. nov. Basionym: *Clytostoma uleanum* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 6: 374. 1915. TYPE: Brazil. Acre: Alto Acre, River São Francisco, s.d., *E. Ule 102b* (holotype, B†; isotype, HBG not seen).

Nomenclatural note. Ongoing monographic study of *Bignonia* will clarify the typification of this species (Zuntini, Taylor & Lohmann, in prep.).

Habitat and distribution. This species is found rather frequently in wet and seasonal forest vegetation in Peru (Cusco, Huánuco, Loreto, Madre de Dios, San

Martín, Ucayali), Bolivia, and Brazil (Acre, Minas Gerais, Rondônia).

V. Callichlamys Miq., Linnaea 18: 254. 1845. TYPE: *Callichlamys riparia* Miq., nom. illeg. superfl. [≡ *Callichlamys latifolia* (Rich.) K. Schum.].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, glabrous, covered with lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a simple tendril, tendrils without adhesive disks, without uncinate apices; leaflets coriaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary, a raceme. Flowers zygomorphic, pentamerous; calyx spathaceous, thickly spongy, puberulous externally, with sparse glands; corolla bright yellow, without nectar guides, infundibuliform, straight in tube, coriaceous, puberulous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and glabrous externally, ovules in multiple series on each placenta, stigma lanceolate, glabrous; disk annular. Capsules elliptic, flattened, straight, woody, with valves 2, glabrous, without lenticels, with scattered glands, without wings, smooth, with calyx caducous; seeds winged, with body smooth and glabrous, wings opaque, linear. Figure 13A, B.

Number of species, distribution, and habitat. *Callichlamys* includes one species found in wet to dry forest vegetation from Mexico to Brazil.

The circumscription of *Callichlamys* as a small genus has remained constant since its description, and as recently regarded taxonomically it is monotypic. The phylogeny hypothesis of Bignonieae (Lohmann, 2006) corroborates this characterization of *Callichlamys* as a lineage that has not diversified. *Callichlamys* can be recognized by its spathaceous, thickly spongy calyx (an apomorphy of the genus; Fig. 13A), ovules arranged in several series on each placenta (also an apomorphy), a relatively large (5–10 cm long) bright yellow corolla (Fig. 13A), and distinctive large (more than 20 cm long) woody, elliptic, smooth fruits.

1. Callichlamys latifolia (Rich.) K. Schum, Nat. Pflanzenfam. 4(3b): 223. 1894. *Bignonia latifolia* Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792. *Tabebuia latifolia* (Rich.) DC., Bibl. Univ. Genève sér. 2 17: 131. 1838. *Delostoma latifolium* (Rich.) Splitg., Tijdschr. Natuurl. Gesch. Physiol. 9: 11. 1842. *Callichlamys riparia* Miq., Linnaea 18: 254. 1845, nom. illeg. superfl. TYPE: French Guiana. Rio Kourou, s.d., *J. B. Le Blond s.n.* (lectotype, designated here, P [barcode] P00481534!; isolectotypes, P [barcode] P00481535!, P [barcode] P00481536!).

Nomenclatural note. Original material of the type collection is at P. Three duplicates are deposited there and the best material is here selected as the lectotype.

Habitat and distribution. This species is found frequently and widely in dry, seasonal, and wet lowland to premontane vegetation in Mexico (Chiapas, Oaxaca, Puebla, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Boyacá, Caquetá, César, Chocó, Córdoba, Cundinamarca, La Guajira, Madgalena, Nariño, Risaralda, Santander, Sucre, Tolima, Valle del Cauca), Venezuela (Amazonas, Aragua, Barinas, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Lara, Miranda, Monagas, Táchira, Yaracuy, Zulia), Guyana, Suriname, French Guiana, Ecuador, Peru (Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Bahia, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Pernambuco, Rio de Janeiro, Rondônia, Roraima, São Paulo).

VI. Cuspidaria DC., Biblioth. Universelle Genève, sèr. 2, 17: 125. Oct. 1838, nom. cons., vs. *Cuspidaria* (DC.) Besser (Brassicaceae). TYPE: *Cuspidaria pterocarpa* (Cham.) DC. [= *Cuspidaria convoluta* (Vell.) A. H. Gentry].

Nouletia Endl., Gen. Pl. 1407. 1841. TYPE: *Nouletia pterocarpa* (Cham.) Pichon (lectotype, designated by Pichon [1946: 228]) [= *Cuspidaria convoluta* (Vell.) A. H. Gentry].

Cremastus Miers, Proc. Roy. Hort. Soc. London 3: 187. 1863. TYPE: *Cremastus glutinosus* (DC.) Miers (lectotype, designated by Baillon [1888: 28]) [= *Cuspidaria sceptrum* (Cham.) L. G. Lohmann].

Saldanhaea Bureau, Adansonia 8: 354. 1868, nom. illeg. hom., non *Saldanha* Vell., 1825. TYPE: *Saldanhaea lateriflora* (Mart.) Bureau [≡ *Cuspidaria lateriflora* (Mart.) DC.].

Setilobus Baill., Hist. Pl. 10: 29. 1888. TYPE: *Setilobus bracteatus* Baill. ex Bureau & K. Schum. [≡ *Cuspidaria bracteata* (Baill. ex Bureau & K. Schum.) L. G. Lohmann].

Blepharitheca Pichon, Bull. Soc. Bot. France 92: 224. 1946. TYPE: *Blepharitheca floribunda* (Mart. ex DC.) Pichon [≡ *Cuspidaria floribunda* (Mart. ex DC.) A. H. Gentry].

Tetrastichella Pichon, Bull. Soc. Bot. France 92: 223. 1946. TYPE: *Tetrastichella inaequalis* (DC. ex Splitg.) Pichon [≡ *Cuspidaria inaequalis* (DC. ex Splitg.) L. G. Lohmann].

Paracarpaea (K. Schum.) Pichon, Bull. Soc. Bot. France 92: 223. 1946. *Arrabidaea* sect. *Paracarpaea* K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. TYPE: *Paracarpaea pulchella* (Cham.) Pichon (lectotype, designated by Pichon [1946: 223]) [≡ *Cuspidaria pulchella* (Cham.) K. Schum.].

Sideropogon Pichon, Bull. Soc. Bot. France 92: 223. 1946. TYPE: *Sideropogon lasianthum* (Bureau & K. Schum.) Pichon [≡ *Cuspidaria lasiantha* (Bureau & K. Schum.) L. G. Lohmann].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, pubescent, with sparse lenticels, with interpetiolar glands, with (without) discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves simple or 2- or 3-foliolate (biternately compound in *Cuspidaria inaequalis*), terminal leaflet often replaced by a simple tendril, tendrils without adhesive disks, without uncinate apices; leaflets with glands grouped in axils of veins or sparsely distributed over lamina, without pellucid punctations, with or without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular, shortly 5-lobed, 5-apiculate, or 5-aristate, membranaceous, puberulous or villose externally, with glands clustered near margins; corolla magenta, pink, or red, without nectar guides, infundibuliform (tubular in *C. cinerea*), straight in tube, membranaceous, glabrous externally (villose in *C. cinerea*), without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae forward-curved, pollen in tetrads, colpate, with exine psilate; ovary sessile, smooth and lepidote externally, ovules in 2 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, puberulous, with lenticels, without glands, with or without wings, smooth except with midrib frequently developed into 2 longitudinal ridges, with calyx caducous; seeds winged, with body smooth and glabrous, wings hyaline, linear. Figure 13C–E.

Number of species, distribution, and habitat. *Cuspidaria* includes 19 species found in wet to dry forest and cerrado vegetation from Mexico to Argentina and Paraguay.

Cuspidaria is characterized by its pollen in tetrads (a synapomorphy of the genus), anthers with forward-curved thecae (also found in *Tynanthus* and some species of *Fridericia*), usually cuspidate or aristate calyx lobes, and capsules with the valves marginally thickened (also found in *Lundia* and *Tynanthus*) and the midrib divided into or bordered by two ridges (a synapomorphy of the genus) that are usually winged.

Cuspidaria as circumscribed here includes several species formerly included in *Arrabidaea*, as well as *Pyrostegia cinerea* Bureau & K. Schum (Fig. 13C–E). The relationship between *P. cinerea* and *Cuspidaria* was unexpected but is supported by molecular data (Lohmann, 2006), and these also share morphological characters.

In the vegetative state *Cuspidaria* is easily confused with *Fridericia*, *Lundia*, *Xylophragma*, and *Tynanthus*. *Cuspidaria* can be recognized by its leaflets with pinnate and straight-percurrent venation together with glands grouped in the axils of veins; this combination of characters is not found in the other genera. Additionally *Tynanthus* can be easily distinguished by its trifid tendrils plus a strong clove smell not found in any other genera.

1. Cuspidaria argentea (Wawra) Sandwith, Kew Bull. 9: 606. 1954 [1955]. *Arrabidaea argentea* Wawra, Oestr. Bot. Z. 29: 216. 1879. *Blepharitheca argentea* (Wawra) Pichon, Bull. Soc. Bot. France 92: 224. 1946. *Saldanhaea argentea* (Wawra) J. C. Gomes, Revista Brasil. Biol. 11: 51. 1951. TYPE: Brazil. Piauí: s. loc., s.d., *G. H. Schwarz s.n.* (holotype, W!, W as photo F neg. 32850 at MO-1692867!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Maranhão, Pernambuco, Piauí).

2. Cuspidaria bracteata (Baill. ex Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Setilobus bracteatus* Baill. ex Bureau & K. Schum., Fl. Bras 8(2): 207. 1896. *Cuspidaria bracteata* Bureau ex Baill., Hist. Pl. 10: 29. 1888, nom. nud. invalid. TYPE: Brazil. Minas Gerais: Duas Pontes, 22 May 1882, *A. Glaziou 14119* (lectotype, designated here, P [no #] not seen, P as photocopy at MO-2692711!; isolectotypes, C not seen, C as photos F neg. 22114 at MO-1185530! and MO-1693056!, K [barcode] K000402986!, K as photocopy at MO-2904343!).

Nomenclatural note. The names *Setilobus bracteatus* and *Cuspidaria bracteata* were invalid in their citation, or implied citation, as published by Baillon (1888); the first name was validated later, but the latter name has never been validly published until now and confusion has surrounded both of these. These names both refer to the species treated here, but have also been extensively confused with the name *Saldanhaea bracteata*, which applies to a distinct species; for more information about this particular confusion, see the discussion of *C. cratensis* below. Baillon (1888: 29) explicitly cited only the name "Cuspidaria bracteata Bur.," without any further information and associated only with the description of the genus *Setilobus*, and this has been interpreted as an intent to describe the species *C. bracteata* and also the combination *S. bracteatus*. However, the description of *Setilobus* here cannot serve as a diagnosis for this species, because Baillon presented one description but explicitly noted that *Setilobus* included two species that he did not distinguish from each other: thus neither of these species was fully described or diagnosed here so neither name was validly published. And, Baillon's citation here of only the name "Cuspidaria bracteata" under the entry for *Setilobus* does not meet the requirements for valid publication of a combination or a new species of *Setilobus*, because the explicit association of the genus name with the epithet is required (McNeill et al., 2006, Art. 33.1). The name *S. bracteatus* was validly published only later, when Bureau and Schumann provided a diagnosis for it. They also cited material collected by Glaziou, but no collection number was given. There are two numbered, good-quality Glaziou collections at P that have been annotated as *Setilobus bracteatus*, and each has been considered the type of this name but these appear to be syntypes. *Glaziou 12986A* has been found only at P, lacks detailed locality data, and has two duplicates that have been annotated by P curators as the holotype and isotype. *Glaziou 14119* has one duplicate at P, annotated as the holotype by Gentry, and various duplicates at other herbaria plus detailed locality data. *Glaziou 14119* is here chosen as the type, following Gentry, and the specimen at P is chosen as the lectotype.

Habitat and distribution. This species is found in eastern Brazil (Minas Gerais), but its exact distribution is not well detailed yet, so its habitat cannot be reliably characterized.

3. Cuspidaria cinerea (Bureau ex K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Pyrostegia cinerea* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 223. 1894. *Cuspidaria cinerea* (Bureau ex K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 763. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais, cultivated in Rio de Janeiro, at Quinta da Boa Vista, 28 Feb. 1882, *A. Glaziou 14124* (lectotype, designated by Pool [2008: 498], P [barcode] P00481542 image!, P [barcode] P00481542 as photo F neg. 22143 at MO-1693044!; isolectotypes, C!, P [barcode] P00481543 image!).

Habitat and distribution. This species is found in forest and especially campinas vegetation on white sand substrates in central Brazil (Amazonas, Minas Gerais).

4. Cuspidaria convoluta (Vell.) A. H. Gentry, Taxon 24(2/3): 343. 1975. *Bignonia convoluta* Vell., Fl. Flumin. 248. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 31. 1827 [1831]. TYPE: tab. 31 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in dry forest vegetation in Bolivia, Paraguay, Brazil (Mato Grosso do Sul, Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), and Argentina (Corrientes, Misiones), and is occasionally cultivated elsewhere.

5. Cuspidaria cratensis (J. C. Gomes) A. H. Gentry ex L. G. Lohmann, comb. nov. Basionym: *Saldanhaea cratensis* J. C. Gomes, Arch. Jard. Bot. Rio de Janeiro 9: 227. 1949. TYPE: Brazil, Ceará: Estrada de Fortaleza a Crato, 3 Aug. 1948, *A. P. Duarte 1256* (holotype, RB-68295 [barcode] 536907!; isotype, RB-68295 [barcode] 537292!).

Saldanhaea bracteata Bureau & K. Schum., Fl. Bras. 8(2): 253. 1896 [1897], non *Cuspidaria bracteata* (Bureau & K. Schum.) L. G. Lohmann. TYPE: Brazil. s. loc., s.d., *A. Glaziou 11125* (not located).

Nomenclatural note. The oldest name for this species is *Saldanhaea bracteata*, but that name cannot be transferred into *Cuspidaria* because the name *C. bracteata* is published here for a different species; the name *C. bracteata* is used here for the species to which that name has been previously applied in sched. The next oldest name for this species is *S. cratensis*, which is used here as the basionym for the combination in *Cuspidaria*; the name *C. cratensis* was used by Gentry for this species in sched., but never actually published by him. In the protologue of *S. bracteata*, only one collection, *Glaziou 11125*, was cited. This has not been located

so far, and further study is needed to resolve the typification of this name. In the meantime, the identity of this name is indicated by additional Glaziou collections that were also annotated as *S. bracteata*, both apparently around the time of the publication of this name and by Gentry: *Glaziou 9956*, P not seen, P as photocopy at MO-2904511!; *Glaziou 11222*, C not seen, C as photo F neg. 22115 at MO-1693047).

Bureau and Schumann (1896) described and distinguished two Bignoniaceae species in two different genera that each start with the letter S, and both species were given the epithet "bracteata." These species are *Saldanhaea bracteata* and *Setilobus bracteatus*, and both species are here classified in *Cuspidaria*. These species are distinct morphologically, ecologically, and geographically, but they have been extensively confused, apparently due mainly to nomenclatural confusion between their names. This confusion has resulted in part from their superficially similar published names, and in part from their informal inclusion by various taxonomists in *Cuspidaria* under the same unpublished name "Cuspidaria bracteosa" used for both species These unpublished names in *Cuspidaria* were based on two different basionyms but have the same parenthetical authors and thus appear to be the same name. This unpublished *Cuspidaria* name has been annotated on many herbarium specimens of both species by people who did not realize that two different basionyms were involved here. The species *Setilobus bracteatus* can be recognized by its well-developed inflorescence bracts and foliaceous prophylls, is found in Minas Gerais in southeastern Brazil, and is here called *C. bracteatus*; the species *Saldanhaea bracteatus* has fewer smaller inflorescence bracts and prophylls, is found in northeastern Brazil, and is here called *C. cratensis*.

Habitat and distribution. This species is found in dry caatinga vegetation in northeastern Brazil (Ceará, Paraíba, Piauí, Rio Grande do Norte).

6. **Cuspidaria emmonsii** A. H. Gentry, Novon 2(2): 160. 1992. TYPE: Peru. Ucayali: Coronel Portillo, bosque von Humboldt, Km. 86, Pucallpa–Tingo María rd., 270 m, 8°40′S, 75°0′W, 9 Feb. 1981, *A. H. Gentry, K. Young, S. Libenson, M. Olsen & T. Trucios 31126* (holotype, MO-2946100!; isotypes, AMAZ not seen, USM not seen).

Habitat and distribution. This species is found in wet forest vegetation in Peru (Cusco, Madre de Dios, Ucayali), Bolivia, and Brazil (Amazonas).

7. **Cuspidaria floribunda** (DC.) A. H. Gentry, Brittonia 25(3): 232. 1973. *Adenocalymma floribundum* DC., in A. DC., Prodr. 9: 201. 1845. *Blepharitheca floribunda* (DC.) Pichon, Bull. Soc. Bot. France 92: 224. 1946. *Saldanhaea floribunda* (DC.) Sandwith, Kew Bull. 22: 408. 1968. TYPE: Bolivia. Santa Cruz, s.d., *A. d'Orbigny 583* (holotype, P [barcode] P00481529!; isotype, G-DC!).

Habitat and distribution. This species is found rather frequently in dry to wet forest vegetation in eastern Panama, Colombia (Chocó), Ecuador, Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Rondônia, São Paulo).

8. **Cuspidaria inaequalis** (DC. ex Splitg.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008. *Bignonia inaequalis* DC. ex Splitg., Tijdschr. Naturl. Gescheid. 9: 6. 1842. *Pleonotoma inaequalis* (DC. ex Splitg.) Miers, Proc. Roy. Hort. Soc. London 3: 184. 1863. *Arrabidaea inaequalis* (DC. ex Splitg.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. *Tetrastichella inaequalis* (DC. ex Splitg.), Bull. Soc. Bot. France 92: 223. 1946. TYPE: Suriname. River Parae, Mar., *O. Berklak s.n.* (holotype, P [barcode] P00468532!).

Habitat and distribution. This species is widely and rather frequently found in evergreen lowland to premontane forest vegetation (Gentry, 1997) in Mexico (Chiapas, Veracruz), Belize, Panama, Colombia (Amazonas, Antioquia, Caquetá, Meta, Vaupés), Venezuela (Amazonas, Anzoátegui, Bolívar, Delta Amacuro, Sucre), Trinidad and Tobago, Guyana, Suriname, French Guiana, Peru (Madre de Dios, San Martín, Ucayali), and Brazil (Acre, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia).

9. **Cuspidaria lachnaea** (Bureau) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 272. 2008, as "*lachanea*." *Cremastus lachnaeus* Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 101. 1893 [1894]. *Arrabidaea lachnaea* (Bureau) Sandwith, Kew Bull. 22: 416. 1968. TYPE: Brazil. Piauí: s. loc., 1839, *G. Gardner 2464* (lectotype, designated here, P [barcode] P00468533!, P [barcode] P00468533 as photocopy at MO-2692757!; isolectotypes, P [barcode] P00468534!, P [barcode] P00468535!, P [barcode] P00468536!, W not seen, W as photo F neg. 32860 at MO-1692942!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Gardner 2464* and *Glaziou 9954*. The collection *Glaziou 9954* has not been located, thus the collection *Gardner 2464* is here designated as the type. This collection has various duplicates and the best quality material is here chosen as the lectotype.

Habitat and distribution. This species is found rather widely but infrequently in semideciduous forest (Gentry, 1997), cerrado vegetation, and on rocky outcrops in Venezuela (Amazonas, Apure, Barinas, Bolívar, Táchira), Bolivia, and Brazil (Ceará, Goiás, Maranhão, Minas Gerais, Piauí).

10. Cuspidaria lasiantha (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea lasiantha* Bureau & K. Schum., Fl. Bras. 8(2): 72. 1896. *Sideropogon lasianthum* (Bureau & K. Schum.) Pichon, Bull. Soc. Bot. France 92: 223. 1946. *Fridericia lasiantha* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: Caraça, 10 June 1884, *A. Glaziou 15254* (holotype, P [barcode] P00468537!; isotype, P [barcode] P00481525!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Minas Gerais, Rio de Janeiro).

11. Cuspidaria lateriflora (Mart.) DC., in A. DC., Prodr. 9: 179. 1845. *Tecoma lateriflora* Mart., Flora 24(2, Beibl.): 51. 1841. *Saldanhaea lateriflora* (Mart.) Bureau, Adansonia 8: 355, tab. 11, 12. 1868. TYPE: Brazil. Mato Grosso: Cuiabá, Morro do Ernesto, Sep.–Oct. 1832, *Mart. Herb. Fl. Bras. 532* (lectotype, designated here, BR-876527!; isolectotypes, BR-876494!, BR-876560!, G-DC!, G-DC as photo F neg. 7671 at MO-1692946!, M-86408!, NY [barcode] NY00328963!).

Nomenclatural note. Several specimens of the type collection are deposited in the Martius Herbarium that is now at BR, with no indication by Martius of which is the type. The most representative and complete of these specimens is here chosen as the lectotype.

Habitat and distribution. This species is found in dry to wet forest vegetation in Peru (Madre de Dios, Puno), Bolivia, Paraguay, and Brazil (Acre, Amazonas, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Pernambuco, Rio de Janeiro, Rondônia).

12. Cuspidaria multiflora DC., in A. DC., Prodr. 9: 179. 1845. TYPE: Brazil. Bahia: Caetité, Oct., *C. F. P. von Martius s.n.* (lectotype, designated here, M-86411!, M as photo F neg. 20460 at MO-1692947!; isolectotypes, G-DC!, M-86410!, M as photo F neg. 20460 at MO-1692947!).

Nomenclatural note. In the protologue de Candolle noted that the type of this name was deposited in M. There are two Martius collections there that correspond to this material, one identified as *Cuspidaria multiflora* and the other as *Lundia multiflora*; de Candolle cited both names in the protologue as names that had been used for this species, though only the name *C. multiflora* was accepted and validly published. Therefore these seem to be syntypes and a lectotype is chosen here. The lectotype is the specimen originally identified as *C. multiflora*, which has better flowers and was photographed with the photos distributed widely by the Field Museum.

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Minas Gerais).

13. Cuspidaria octoptera A. H. Gentry, Ann. Missouri Bot. Gard. 64(2): 314. 1977 [1978]. TYPE: Brazil. s. loc., s.d., *J. Nadeaud s.n.* (holotype, P [barcode] P00481523!; isotypes, MO-4939540!, P [barcode] P00481524!)

Habitat and distribution. This species is found in dry forest vegetation in eastern Brazil (Minas Gerais, Pernambuco, Rio de Janeiro, São Paulo).

14. Cuspidaria pulchella (Cham.) K. Schum., Nat. Pflanzenfam. 4(3b): 216. 1894. *Bignonia pulchella* Cham., Linnaea 7: 663. 1832 [1833]. *Arrabidaea pulchella* (Cham.) Bureau, in J. E. B. Warming, Lagoa Santa 270. 1892. *Paracarpaea pulchella* (Cham.) Pichon, Bull. Soc. Bot. France 92: 223. 1946. *Fridericia pulchella* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia pulchella* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *F. Sellow 5349* (holotype, LE not seen; isotypes, B-18453†, B as photo F neg. 18453 at MO-1692853!, K!).

Habitat and distribution. This species is found in cerrado vegetation in Paraguay and Brazil (Mato Grosso do Sul, Minas Gerais, Paraná, São Paulo).

15. Cuspidaria pulchra (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia pulchra* Cham., Linnaea 7: 708. 1832 [1833]. *Cremastus pulcher* (Cham.) Bureau, Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd. 6: 270. 1892. *Arrabidaea pulchra* (Cham.) Sandwith, Kew Bull. 22: 416. 1968. *Cuspidaria pulchra* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *F. Sellow 1609* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18488 at MO-1692904!, K!, NY [barcode] NY00313148!, NY [barcode] NY00313148 as photocopy at MO-2927266!).

Habitat and distribution. This species is found in cerrado vegetation and on dry rocky outcrops in Bolivia and Brazil (Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, São Paulo).

16. Cuspidaria sceptrum (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia sceptrum* Cham., Linnaea 7: 710. 1832 [1833]. *Petastoma sceptrum* (Cham.) Miers, Proc. Roy. Hort. Soc. 3: 195. 1863. *Cremastus sceptrum* (Cham.) Bureau & K. Schum., Fl. Bras. 8(2): 216. 1896. *Arrabidaea sceptrum* (Cham.) Sandwith, Kew Bull. 22: 416. 1968. *Cuspidaria sceptrum* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. Chapada, 1814–1831, *F. Sellow s.n.* (holotype, LE not seen; isotypes, presumably B†, US-282523 image!, US-286309 image!).

Nomenclatural note. The collection locality of the Sellow specimen cited in the protologue was given simply as Chapada. This species' range includes several different places that are each called Chapada, and it is unknown in which Chapada this was collected.

Habitat and distribution. This species is found in cerrado vegetation and on dry rocky outcrops in Bolivia and Brazil (Bahia, Distrito Federal, Goiás, Mato Grosso, Minas Gerais, Paraná, Rondônia, São Paulo).

17. Cuspidaria simplicifolia DC., Biblioth. Universelle Genève, sér. 2, 17: 125. 1838. TYPE: Brazil. Bahia: Sierra d'Apurna près le Rio Saint-François, 1838, *J. S. Blanchet 2801* (holotype, G-DC [barcode] G00133399!; isotypes, MO-1998979!, NY [barcode] NY00328767!, P [barcode] P00608082!, P [barcode] 608083!, P [barcode] P00608084!).

Cuspidaria puberula Mart. ex DC., in A. DC., Prodr. 9: 178. 1845, syn. nov. *Panterpa puberula* (Mart. ex DC.) Miers, Proc. Roy. Hort. Soc. London 3: 196. 1863. *Arrabidaea puberula* (Mart. ex DC.) Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 99. 1893 [1894]. *Blepharitheca puberula* (Mart. ex DC.) Pichon, Bull. Soc. Bot. France 92: 224. 1946. *Saldanhaea puberula* (Mart. ex DC.) J. C. Gomes, Revista Brasil. Biol. 11: 51. 1951. TYPE: Brazil. Bahia: Monte Santo, 1 Apr., *C. F. P. von Martius 2269* (holotype, G-DC!; isotypes, M not seen, M as photo F neg. 20443 at K! and at MO-1692851!).

Nomenclatural note. Study of the type specimens shows the names *Cuspidaria simplicifolia* and *C. puberula* apply to the same species, and these names are accordingly synonymized here.

Habitat and distribution. This species is found in dry forest and caatinga vegetation in Bolivia and Brazil (Bahia, Ceará, Minas Gerais, Pernambuco, Piauí, Rio de Janeiro, São Paulo).

18. Cuspidaria subincana A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 52, fig. 1b. 1976. TYPE: Brazil. Amazonas: 2–5 km N of Manaus–Itacoatiara Rd., near Preto da Eva, Km. 79, 100–200 m, 24 Nov. 1974, *A. H. Gentry 12825* (holotype, INPA not seen; isotypes, MG not seen, MO-2251768!, RB-185814 [barcode] 536879!, RB-185814 [barcode] 537282!).

Habitat and distribution. This species is found in wet premontane forest vegetation (Gentry, 1997) in Colombia (Meta), Venezuela (Bolívar), Suriname, and Brazil (Amazonas, Rondônia).

19. Cuspidaria weberbaueri (Sprague) A. H. Gentry, Brittonia 25(3): 233. 1973. *Arrabidaea weberbaueri* Sprague, Bot. Jahrb. Syst. 42: 175. 1908. *Saldanhaea weberbaueri* (Sprague) Sandwith, Kew Bull. 22: 408. 1968. TYPE: Peru. Junín: Tarma, La Merced in Chanchamayothal, 1000 m, s.d., *A. Weberbauer 1934* (holotype, presumably B†; isotype, G-8923!, G as photo F neg. 26177 at MO-1692865!).

Nomenclatural note. Further study is needed before the typification of this species can be clarified.

Habitat and distribution. This species is found in dry forest vegetation in the Huallaga and Chanchamayo valleys of central Peru (Junín, San Martín; Gentry, 1992a).

VII. Dolichandra Cham., Linnaea 7: 657. 1832 [1833], emend. L. G. Lohmann. TYPE: *Dolichandra cynanchoides* Cham.

Macfadyena A. DC., Prodr. 9: 179. 1845, syn. nov. TYPE: *Macfadyena uncinata* (G. Mey.) A. DC. [= *Dolichandra uncata* (Andrews) L. G. Lohmann].

Doxantha Miers, Proc. Roy. Hort. Soc. London 3: 189. 1863. TYPE: *Doxantha unguis-cati* (L.) Miers [≡ *Dolichandra unguis-cati* (L.) L. G. Lohmann].

Melloa Bureau, Adansonia 8: 379. 1868, syn. nov. TYPE: *Melloa populifolia* (DC.) Bureau (lectotype, designated by Baillon [1888: 26]). [= *Dolichandra quadrivalvis* (Jacq.) L. G. Lohmann].

Parabignonia Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 229. 1894, syn. nov. TYPE: *Parabignonia maximillianii* (Mart. ex DC.) Bureau ex K. Schum. [= *Dolichandra unguiculata* (Vell.) L. G. Lohmann].

Paradolichandra Hassl., Bull. Herb. Boissier, sér. 2, 7: 718. 1907, syn. nov. TYPE: *Paradolichandra chodatii* Hassl. [≡ *Dolichandra chodatii* (Hassl.) L. G. Lohmann].

Microbignonia Kraenzl., Notizbl. Königl. Bot. Gart. Berlin 6: 380. 1915. TYPE: *Microbignonia auristellae* Kraenzl. [= *Dolichandra unguis-cati* (L.) L. G. Lohmann].

Batocydia Mart. ex Britton, Sci. Surv. Porto Rico & Virgin Islands 6: 194. 1925, nom. illeg. superfl. TYPE: *Batocydia unguis-cati* (L.) Mart. ex Britton, as "*Batocydia unguis*." [≡ *Dolichandra unguis-cati* (L.) L. G. Lohmann].

Lianas, with dimorphic juvenile growth, without strong odor; stems with multiple dissected phloem wedges in cross-section, pith solid; branchlets cylindrical (tetragonal), glabrous, with or without lenticels, with or without interpetiolar glands, with (without) discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds subulate, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, with uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary, a congested cyme or thyrse (umbellate groups of cymes). Flowers zygomorphic, pentamerous; calyx cupular and irregularly lobed or spathaceous, membranaceous, glabrous to puberulent externally, without glands; corolla yellow or red, without nectar guides, tubular or infundibuliform, straight in tube, membranaceous, glabrous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included or exserted, anthers glabrous, thecae straight, pollen in monads, colpate, with exine psilate; ovary sessile, smooth and glabrous to puberulous externally, ovules in multiple (1) series on each placenta, stigma rhombic, glabrous; disk annular and lobed. Capsules linear (elliptic), flattened or inflated, straight, coriaceous (woody), with valves 2 and partially divided longitudinally or 4, glabrous, with or without lenticels, without glands, without wings, smooth, with calyx persistent; seeds winged, with body smooth and glabrous, wings hyaline, linear.

Number of species, distribution, and habitat. *Dolichandra* includes eight species found in wet to dry forest vegetation from the southeastern U.S.A., Mexico, and the Antilles to Argentina.

Dolichandra is circumscribed broadly here, to include *Parabignonia*, *Melloa*, and *Macfadyena*. These genera have long been considered related, but were separated based primarily on flower color (red in *Dolichandra*, yellow in *Macfadyena* and *Melloa*, and red or yellow in *Parabignonia*) and fruit shape (elliptic in *Melloa* and *Dolichandra*, vs. linear in *Macfadyena* and *Parabignonia*). For example, Gentry (1973a: 237) observed "Although *Melloa* is monotypic and closely related to *Macfadyena*, I prefer to retain it as a distinct genus for the present. Its thick-walled, elliptic-oblong fruit, with each valve breaking in the middle at dehiscence, is certainly different from the linear, thin-walled fruits of *Macfadyena* from which it must have been derived." However, these four genera form a strongly supported monophyletic group in the phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006; Fig. 2), and this clade is here treated as a single genus. This broadly circumscribed *Dolichandra* is distinguished by its multiple dissected phloem wedges (Santos, 1995; a synapomorphy of the genus), uncinate or clawlike tendrils (another synapomorphy), colpate pollen with a psilate exine (Gentry & Tomb, 1979), and 4-parted fruits (another synapomorphy). Additionally *Dolichandra* is characterized by dimorphic growth with the juvenile form attaching by its uncinate tendrils, subulate prophylls of the axillary buds, congested-cymose inflorescences, and a lobed nectar disk. As noted previously, flower color and fruit shape are highly homoplasious in Bignonieae, and these vary markedly within *Dolichandra*.

1. Dolichandra chodatii (Hassl.) L. G. Lohmann, comb. nov. Basionym: *Paradolichandra chodatii* Hassl., Bull. Herb. Boissier, sér. 2, 7: 720. 1907. *Parabignonia chodatii* (Hassl.) A. H. Gentry, Ann. Missouri Bot Gard. 66(4): 785. 1979 [1980]. *Dolichandra chodatii* (Hassl.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1602. 2008, nom. nud. invalid. *Dolichandra chodatii* (Hassl.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Paraguay. Sierra de Amambay, Picada Esperanza, 1907–1908, *E. Hassler 10281* (holotype, G!, G as photo F neg. 26200 at MO-1693014!; isotype, NY-328894!).

Habitat and distribution. This species is found in moist to dry forest vegetation in eastern Bolivia, Paraguay, southern Brazil (Paraná), and northern Argentina (Jujuy, Salta).

2. Dolichandra cynanchoides Cham., Linnaea 7: 658. 1832 [1833]. *Macfadyena cynanchoides* (Cham.) Morong, Ann. New York Acad. Sci. 7: 187. 1893. TYPE: Brazil. s. loc., s.d., *F. Sellow 942* (holotype, LE not seen; isotype, B†, B as F neg. 18431 at MO-1692954!).

Habitat and distribution. This species is found in dry to wet forest vegetation in Bolivia, Paraguay, Brazil (Paraná, Rio Grande do Sul, Santa Catarina), Uruguay, and Argentina (Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, Misiones, Salta, Santa Fe, Tucumán), and is cultivated in tropical and warm temperate regions worldwide.

3. Dolichandra dentata (K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Macfadyena dentata* K. Schum., Nat. Pflanzenfam. 4(3b): 227. 1894. *Dolichandra dentata* (K. Schum.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1602. 2008, nom. nud invalid. *Dolichandra dentata* (K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. Betw. Campo Novo & Palmeira, s.d., *G. Niederlein 188* (holotype, B†); Uruguay, Concepción del Uruguay, Nov 1877, *P. G. Lorentz s.n.* (lectotype, designated here, K [barcode] K000449794 image!).

Nomenclatural note. Schumann (1894) reported that the type of *Macfadyena dentata* was from Brazil without further details, but several collections of this species were listed by Bureau and Schumann (1896: 292–293). Only one of these, a collection by Niederlein, is from Brazil and this is assumed to be the type of this species; however, a specimen of this presumably deposited at B was destroyed and no duplicates have been located. The other specimens cited by Bureau and Schumann were from Uruguay near Villa de Minas, *Sello 276* and *Sello 853*; from Uruguay along the Rio Santa Luzia, *Kuntze s.n.*; from Uruguay near Concepcion, *Lorentz s.n.*; and from an undesignated location along the Rio Paraná, *Tweedie s.n.* The last two of these collections have been located at K, and the collection by Lorentz is more complete and representative and is here chosen as the lectotype.

Habitat and distribution. This species is found in humid to dry forest vegetation in Paraguay, Brazil (Paraná, Rio Grande do Sul, Santa Catarina), Uruguay, and Argentina (Buenos Aires, Córdoba, Corrientes, Entre Ríos, Misiones).

4. Dolichandra quadrivalvis (Jacq.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 273. 2008. *Bignonia quadrivalvis* Jacq., Fragm. Bot. 37, tab. 40, fig. 3. 1800 [1809]. *Melloa quadrivalvis* (Jacq.) A. H. Gentry, Brittonia 25(3): 237. 1973, as "quadrivalva." TYPE: tab. 40, fig. 3 in Jacq., Fragm. Bot. 37, 1800 [1809] (lectotype, designated here).

Nomenclatural note. No Jacquin collections of this species have been found, in spite of two searches throughout the W herbarium where he worked. The illustration presented in the original description of this species is diagnostic and is here selected as the lectotype.

Habitat and distribution. This species is found widely in dry to wet forests and particularly in seasonal lowland forest vegetation, in Mexico (Chiapas, Guerrero, Hidalgo, Jalisco, Michoacán, Oaxaca, Puebla, Querétaro, Tamaulipas, Veracruz, Yucatán), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Colombia (Atlántico, Bolívar, César, Cundinamarca, Magdalena, Tolima), Venezuela (Anzoátegui, Apure, Aragua, Barinas, Cojedes, Distrito Federal, Guárico, Lara, Monagas, Portuguesa, Zulia), Guyana, Peru (Madre de Dios, Ucayali), Bolivia, Paraguay, Brazil (Bahia, Ceará, Espírito Santo, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo), Uruguay, and Argentina (Chaco, Corrientes, Entre Ríos, Jujuy, Misiones, Salta).

5. Dolichandra steyermarkii (Sandwith) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 273. 2008. *Parabignonia steyermarkii* Sandwith, Bol. Soc. Venez. Ci. Nat. 26: 446, fig. 11. 1966. TYPE: Venezuela. Bolívar: Km. 119 S of El Dorado, 1030 m, 12 Jan. 1964, *J. A. Steyermark et al. 93003* (holotype, K!; isotypes, F-1653425 image!, S not seen, VEN not seen).

Habitat and distribution. This species is found in wet and cloud forest vegetation (Gentry, 1997) in Costa Rica, Panama, Venezuela (Bolívar, Delta Amacuro, Sucre), Guyana, Suriname, French Guiana, Ecuador, Peru (Loreto), and Brazil (Acre, Pará).

6. Dolichandra uncata (Andrews) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 273. 2008. *Bignonia uncata* Andrews, Bot. Repos. 8: tab. 530. 1808. *Spathodea uncata* (Andrews)

Spreng., Syst. Veg. 2: 835. 1825. *Doxantha uncata* (Andrews) Miers, Proc. Roy. Hort. Soc. London 3: 190. 1863. *Macfadyena uncata* (Andrews) Sprague & Sandwith, Receuil Trav. Bot. Néerl. 34: 215. 1937. TYPE: tab. 530 in Bot. Reposit. 8, 1808, illustration based on a cultivated specimen from Cayenne [French Guiana] brought to England by Lord Seaforth (lectotype, designated by Howard [1989: 325]).

Habitat and distribution. This species is found widely and frequently in swampy and riverside forest vegetation (Gentry, 1997) in Mexico (Quintana Roo, Tabasco, Veracruz), the Greater Antilles (Cuba), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Atlántico, Bolívar, Boyacá, Chocó, Córdoba, La Guajira, Magdalena, Meta, Valle del Cauca), Venezuela (Amazonas, Apure, Barinas, Bolívar, Carabobo, Delta Amacuro, Guárico, Miranda, Monagas, Sucre, Yaracuy, Zulia), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Puno, San Martín, Ucayali), Bolivia, Paraguay, Brazil (Amapá, Amazonas, Maranhão, Mato Grosso, Minas Gerais, Pará, Paraná, Rio de Janeiro, Rio Grande do Sul, São Paulo), Uruguay, and Argentina (Buenos Aires, Chaco, Corrientes, Formosa, Jujuy, Misiones).

7. Dolichandra unguiculata (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia unguiculata* Vell., Fl. Flumin. 248. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 33. 1827 [1831]. *Doxantha unguiculata* (Vell.) Miers, Proc. Roy. Hort. Soc. London 3: 190. 1863. *Parabignonia unguiculata* (Vell.) A. H. Gentry, Taxon 24(4): 343. 1975. *Dolichandra unguiculata* (Vell.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1603. 2008, nom. nud. invalid. *Dolichandra unguiculata* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: tab. 33 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, São Paulo).

8. Dolichandra unguis-cati (L.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 273. 2008. Basionym: *Bignonia unguis-cati* L., Sp. Pl. 2: 623. 1753. *Doxantha unguis-cati* (L.) Miers, Proc. Roy. Hort. Soc. London 3: 189. 1863, as "*unguis*." *Batocydia unguis-cati* (L.) Mart. ex Britton, Brooklyn Bot. Gard. Mem. 1: 90. 1918, nom. nud invalid. *Batocydia unguis-cati* (L.) Mart. ex Britton, Sci. Surv. Porto Rico & Virgin Islands 6(2): 194. 1925, nom. illeg. superfl., as "*unguis*." *Macfadyena unguis-cati* (L.) A. H. Gentry, Brittonia 25(3): 236. 1973. TYPE: tab. 94 in Plumier, Descr. Pl. Amer., 1693 (lectotype, designated by Nasir [1979: 18]).

Habitat and distribution. This species is widely and commonly found in dry to humid lowland forests in the southeastern United States (Florida), Mexico (Baja California Sur, Campeche, Chiapas, Guerrero, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Yucatán), the Antilles (Antigua, Bahamas, Barbados, Barbuda, Cuba, Dominica, Dominican Republic, Grenada, the Grenadines, Guadeloupe, Haiti, Martinique, Montserrat, Puerto Rico, Saba, San Andrés-Providencia, St. Eustatius, St. Lucia, St. Martin, St. Vincent, Virgin Islands), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Atlántico, Bolívar, Boyacá, Caldas, César, Chocó, Córdoba, Cundinamarca, Guaviare, La Guajira, Magdalena, Meta, Sucre), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Yaracuy, Zulia), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, Paraguay, Brazil (Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo, Sergipe), Uruguay, and Argentina (Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, Misiones, Salta, Santa Fe, Tucumán), and is cultivated in warm regions worldwide and is an invasive weed in eastern Australia. This is the most commonly collected species of this tribe.

VIII. Fridericia Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13(2): 7. 1827, emend. L. G. Lohmann. TYPE: *Fridericia speciosa* Mart. (lectotype, designated by Schumann [1894: 222]).

Arrabidaea DC., Biblioth. Univers. Genève, sér. 2, 17: 126. 1838, syn. nov. TYPE: *Arrabidaea rego* (Vell.) DC. [≡ *Fridericia rego* (Vell.) L. G. Lohmann].

Pentelesia Raf., Sylva Tellur. 146. 1838. TYPE: *Pentelesia discolor* Raf., nom. superfl. illeg. [≡ *Fridericia carichanensis* (Kunth) L. G. Lohmann].

Vasconcellia Mart., Flora 24(2, Beibl.): 12. 1841, hom. illeg., syn. nov., non *Vasconcella* A. St. Hil. (1837), nom. superfl. illeg. TYPE: *Vasconcellia rego* (Vell.) Mart. [≡ *Fridericia rego* (Vell.) L. G. Lohmann].

Panterpa Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. TYPE: *Panterpa leucopogon* (Cham.) Miers [≡ *Fridericia leucopogon* (Cham.) L. G. Lohmann].

Petastoma Miers, Proc. Roy. Hort. Soc. London 3: 194. 1863. TYPE: *Petastoma samydoides* (Cham.) Miers [≡ *Fridericia samydoides* (Cham.) L. G. Lohmann].

Neomacfadya Baill., Hist. Pl. 10: 26. 1888. *Neomacfadyena*, orth. var. TYPE: *Neomacfadya podopogon* (DC.) Baill. ex K. Schum. [≡ *Fridericia podopogon* (DC.) L. G. Lohmann].

Paramansoa Baill., Hist. Pl. 10: 27. 1888. TYPE: *Paramansoa grosourdyana* Baill. [≡ *Fridericia grosourdyana* (Baill.) L. G. Lohmann].

Chasmia Schott ex Kuntze, Revis. Gen. Pl. 2: 479. 1891, nom. superfl. illeg., syn. nov. *Chasmia* Schott ex Spreng., Syst. Veg. 4(2): 409. 1827, nom. nud. invalid. TYPE: *Chasmia rego* (Vell.) Kuntze [≡ *Fridericia rego* (Vell.) L. G. Lohmann].

Stenosiphanthus A. Samp., Bol. Mus. Nac. Rio de Janeiro 12(3, 4): 84. 1936. TYPE: *Stenosiphanthus duckei* A. Samp. [= *Fridericia lauta* (Bureau & K. Schum.) L. G. Lohmann].

Scobinaria Siebert, Publ. Carnegie Inst. Wash. 522: 408. 1940. TYPE: *Scobinaria verrucosa* (Standl.) Seibert [= *Fridericia schumanniana* (Loes.) L. G. Lohmann].

Piriadacus Pichon, Bull. Soc. Bot. France 92: 225. 1946. *Alsocydia* Mart. ex J. C. Gomes, Revista Brasil. Biol. 11: 49. 1951, nom. superfl. illeg. TYPE: *Piriadacus erubescens* (DC.) Pichon [≡ *Fridericia erubescens* (DC.) L. G. Lohmann].

Lianas or shrubs, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, glabrous to pubescent, with or without lenticels, with (without) interpetiolar glands, with or without interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves 1- to 3-foliolate, terminal leaflet often replaced by a simple tendril, tendrils without adhesive disks, without uncinate apices; leaflets without glands or with glands sparsely distributed over lamina or grouped in axils of veins, without pellucid punctations, usually with domatia on abaxial surface, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary and/or terminal, a thyrse or compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular, tubular, or urceolate, shortly 5-lobed, 5-apiculate, or bilabiate, membranaceous or coriaceous, lepidote or puberulous externally, without glands or with solitary glands near margins; corolla magenta or pink (red, white), without nectar guides, tubular or infundibuliform, straight in tube, membranaceous or coriaceous, villose (glabrous) externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight or forward-curved, pollen in monads, colpate, with exine psilate (reticulate in *Fridericia erubescens*); ovary sessile, smooth and lepidote externally, ovules in 1 series on each placenta, stigma elliptic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, lepidote, with lenticels (without in *F. erubescens*), without glands, without wings (with wings in *F. erubescens*), smooth (tuberculate in *F. verrucosa*), with calyx caducous; seeds winged, with body smooth and glabrous, wings hyaline (opaque in *F. speciosa*), linear or elliptic. Figures 14, 15.

Nomenclatural note. Martius described the new genus *Fridericia* with two species and did not designate either of them as its type. Schumann recognized one species of *Fridericia* and synonymized these two names, which is here considered an effective lectotypification.

Number of species, distribution, and habitat. *Fridericia* includes 67 species found in wet to dry forest, cerrado, and caatinga vegetation from Mexico to Argentina and southern Brazil.

Fridericia is here circumscribed much more broadly than previously and is characterized by triangular and minute prophylls of the axillary buds, the presence of interpetiolar glands (Fig. 14F), simple tendrils, thyrsoid inflorescences (Fig. 14E), pink flowers, lepidote ovaries with a single series of ovules on each placenta, and lepidote lenticellate fruits that lack glands.

As previously circumscribed, *Fridericia* was monotypic and its relationships to other taxa in this tribe were unclear. In the phylogenetic hypothesis of tribe Bignonieae (Lohmann, 2006), *Fridericia* is nested within a clade that also includes many of the species that have been classified in *Arrabidaea*. *Arrabidaea* has long been the largest, most polymorphic, and most taxonomically confused genus of Bignonieae. Unsurprisingly, the phylogenetic analysis found that *Arrabidaea* in its previous circumscription was polyphyletic with its species distributed among four clades: *Fridericia–Arrabidaea* s. str., *Cuspidaria*, *Tanaecium*, and *Xylophragma*. The *Fridericia–Arrabidaea* s. str. clade is well supported and includes *A. rego* (Vell.) DC., the type of *Arrabidaea*, along with the majority of species that have been classified in *Arrabidaea* and the genera *Piridicus* and *Fridericia*. Of these *Fridericia* is the oldest name and is thus the name of this combined group. The other species previously included in *Arrabidaea* are here variously classified in *Tanae-*

cium (species with foliaceous or bromeliad-like prophylls of the axillary buds), *Cuspidaria* (species with forward-curved anthers), and *Xylophragma* (species with multiple series of ovules per placenta).

Relationships among species within *Fridericia* are still unclear. The phylogenetic hypothesis of Bignonieae (Lohmann, 2006) suggests that the species that were formerly separated in *Petastoma* and *Scobinaria* together form a monophyletic group, but no other groups are separated. The species sampling in this analysis is not broad or detailed enough to confidently identify lineages within *Fridericia*, and more detailed study is underway (Lohmann, 2003; Lohmann et al., in prep.).

1. Fridericia arthrerion (Mart.) L. G. Lohmann, comb. nov. Basionym: *Bignonia arthrerion* Mart., Flora 24(2, Beibl.): 47. 1841. *Distictis arthrerion* (Mart.) DC., in A. DC., Prodr. 9: 191. 1845. *Arrabidaea arthrerion* (Mart.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Fridericia arthrerion* (Mart.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Cuiabá, Feb. 1833, *A. Silva Manso 18* (*Herb. Fl. Brasil. 515*) (holotype, M-86391!, M as photo K neg. 20437 at MO-1692771!; isotypes, BR-880472!, G-14139!, G-DC!, MO-2005583!, P [barcode] P00468550!).

Habitat and distribution. This species is found in dry forest vegetation in eastern Bolivia and southwestern Brazil (Mato Grosso).

2. Fridericia bahiensis (Schauer ex DC.) L. G. Lohmann, comb. nov. Basionym: *Vitex bahiensis* Schauer ex DC., in A. DC., Prodr. 11: 687. 1847. *Arrabidaea bahiensis* (Schauer ex DC.) Sandwith & Moldenke, Revista Sudamer. Bot. 4: 15. 1937. *Fridericia bahiensis* (Schauer ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Igreja Velha, 1841, *J. S. Blanchet 3274* (holotype, G-DC!; isotypes, F-876595 image!, G-14128!, P [barcode] P00468551!, P [barcode] P00468552!, P [barcode] P00468553!).

Habitat and distribution. This species is found in cerrado vegetation and on dry rocky outcrops in eastern Brazil (Bahia, Minas Gerais, Piauí, Rio de Janeiro).

3. Fridericia bracteolata (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia bracteolata* DC., in A. DC., Prodr. 9: 157. 1845. *Arrabidaea bracteolata* (DC.) Sandwith, Receuil Trav. Bot. Néerl 34: 215. 1937. *Fridericia bracteolata* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *C. F. P. von Martius s.n.* (holotype, G-DC!; isotype, M-86397!).

Habitat and distribution. This species is found in wet lowland forests in Colombia (Amazonas, Nariño), Ecuador, Peru (Loreto), and Brazil (Amazonas).

4. Fridericia candicans (Rich.) L. G. Lohmann, comb. nov. Basionym: *Bignonia candicans* Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792. *Arrabidaea candicans* (Rich.) DC., in A. DC., Prodr. 9: 185. 1845. *Fridericia candicans* (Rich.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1604. 2008, nom. nud. invalid. *Fridericia candicans* (Rich.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 764. 2010, nom. nud. invalid. TYPE: French Guiana. Cayenne, 1792, *J. B. Le Blond 290* (holotype, G-8805!, G-8805 as photo F neg. 26169 at MO-1692778!).

Habitat and distribution. This species is found widely in wet lowland to montane forest vegetation, often on white sand substrates in South America (Gentry, 1997), in Mexico (Tabasco, Veracruz), Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Arauca, Atlántico, Bolívar, Caldas, Cauca, Chocó, Córdoba, Cundinamarca, Huila, La Guajira, Magdalena, Meta, Norte de Santander, Putumayo, Santander, Sucre, Tolima), Venezuela (Aragua, Barinas, Bolívar, Carabobo, Distrito Federal, Mérida, Miranda, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia), Guyana, Suriname, French Guiana, Ecuador, Peru (Loreto, San Martín, Ucayali), Bolivia, Paraguay, and Brazil (Acre, Amapá, Amazonas, Ceará, Mato Grosso, Pará).

5. Fridericia carichanensis (Kunth) L. G. Lohmann, comb. nov. Basionym: *Bignonia carichanensis* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 137. 1818 [1819]. *Pentelesia discolor* Raf., Sylva Tellur. 78. 1838, nom. illeg. superfl. *Arrabidaea carichanensis* (Kunth) Bureau & K. Schum., Fl. Bras. 8(2): 62. 1896. TYPE: Venezuela. Bolívar: betw. Encaramadae & Carichana, close to River Orinoco, May, *F. W. H. A. von Humboldt & A. J. A. Bonpland 831* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39419 at MO-1692924!; isotype, B-W-11414!).

Nomenclatural note. The names *Bignonia carichanensis* and *B. verrucosa* Kunth were published simultaneously, with both names applying to the

same species. These taxa were previously synonymized by Gentry (1982), who chose the first name.

Habitat and distribution. This species is found in seasonally flooded lowland forest vegetation (Gentry, 1997) in Colombia (Vichada) and Venezuela (Amazonas, Anzoátegui, Apure, Bolívar, Guárico).

6. Fridericia caudigera (S. Moore) L. G. Lohmann, comb. nov. Basionym: *Bignonia caudigera* S. Moore, Trans. Linn. Soc. London, Bot. 4: 415. 1895. *Arrabidaea caudigera* (S. Moore) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 43. 1976. *Fridericia caudigera* (S. Moore) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1604. 2008, nom. nud. invalid. *Fridericia caudigera* (S. Moore) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Corumbá, Jan. 1891–1892, *S. Moore 971* (holotype, BM!).

Habitat and distribution. This species is found in dry forest vegetation in Bolivia, Paraguay, Brazil (Acre, Bahia, Ceará, Espírito Santo, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraná, Santa Catarina, São Paulo), and Argentina (Corrientes, Misiones).

7. Fridericia celastroides (Bureau ex K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea celastroides* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Fridericia celastroides* (Bureau ex K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: near Jacobina, s.d., *J. S. Blanchet 3419* (lectotype, designated here, G-8903!; isolectotypes, P [barcode] P00468568!, P [barcode] P00468569!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Blanchet 3419* and *Glaziou 14110*. Good material of the collection *Blanchet 3419* was found both at P (two duplicates) and G, while material of *Glaziou 14110* was found at MO (MO-2167736) and K (photocopy at MO-2904336!). No locality information was given in the protologue for the Glaziou collection, but its label gives a general collecting locality in the region of Rio de Janeiro. The *Blanchet 3419* collection is preferred due to its more accurate collection locality and the higher number of duplicates, and the specimen at G is chosen as the lectotype because it includes the largest number of flowers.

Habitat and distribution. This species is found in dry forest and cerrado vegetation in eastern Brazil (Bahia, Minas Gerais, Rio de Janeiro).

8. Fridericia chica (Bonpl.) L. G. Lohmann, comb. nov. Basionym: *Bignonia chica* Bonpl., Pl. Aequinoct. 1: 107, tab. 31, fig. 1. 1807. *Lundia chica* (Bonpl.) Seem., Bot. Voy. Herald 180. 1854. *Arrabidaea chica* (Bonpl.) Verl., Rev. Hort. 40: 154. 1868. *Fridericia chica* (Bonpl.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1604. 2008, nom. nud. invalid. *Fridericia chica* (Bonpl.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Venezuela. Amazonas: ad amnen Cassiquiare et ad flumen Orenocum inter Esmeraldas et Maypure, s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P [barcode] P00136295!; isotypes, B-W-11422!, K!).

Habitat and distribution. This species is widely and frequently found in wet to seasonal, lowland to montane forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Oaxaca, Veracruz), the Antilles (Dominica, Dominican Republic, Puerto Rico, Virgin Islands), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Bolívar, Chocó, Córdoba, La Guajira, Magdalena, Meta, Nariño, Putumayo, Santander, Tolima, Valle del Cauca), Venezuela (Amazonas, Apure, Aragua, Barinas, Bolívar, Carabobo, Delta Amacuro, Lara, Portuguesa, Táchira, Trujillo, Yaracuy, Zulia), French Guiana, Ecuador, Peru (Cajamarca, Cusco, Loreto, Madre de Dios, San Martín), Bolivia, Paraguay, Brazil (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Catarina, São Paulo), Uruguay, and Argentina (Corrientes, Misiones).

9. Fridericia cinerea (Bureau ex K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea cinerea* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Fridericia cinerea* (Bureau ex K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Jacobina, Serra do Açuruá, Rio São Francisco, 1838, *J. S. Blanchet 2856* (lectotype, designated here, P [barcode] P00468558!; isolectotypes, NY [barcode] NY00313083!, NY [barcode] NY00313083 as photocopy at MO-2927265!, P [barcode] P00468557!, W not seen, W as photo F neg. 32953 at MO-1692871!).

Nomenclatural note. Original material of the type collection of this species is at P. Two duplicates are deposited there and the best material is here selected as the lectotype.

Habitat and distribution. This species is found in dry forest vegetation in Venezuela (Bolívar), Guyana, Suriname, Bolivia, and Brazil (Bahia, Ceará, Minas Gerais, Pará).

10. Fridericia cinnamomea (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia cinnamomea* DC., in A. DC., Prodr. 9: 164. 1845. *Arrabidaea cinnamomea* (DC.) Sandwith, Candollea 7: 248. 1936. *Fridericia cinnamomea* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Cuiabá, Nov. 1832, *A. Silva Manso s.n.* (holotype, G-DC!, G-DC as photo F neg. 7632 at MO-1692888!).

Habitat and distribution. This species is found widely in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Amazonas, Bolívar), French Guiana, Peru (Loreto, Pasco San Martín, Ucayali), Bolivia, and Brazil (Amazonas, Bahia, Goiás, Maranhão, Mato Grosso, Pará, Roraima).

11. Fridericia claussenii (A. DC.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea claussenii* A. DC., Prodr. 9: 186. 1845, as "*clausseni*." *Petastoma claussenii* (A. DC.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Fridericia claussenii* (A. DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: s. loc., 1838, *P. Claussen 197* (lectotype, designated here, G-DC!; isolectotypes, K [barcode] K000449113!, MO-2245222!, NY [barcode] NY00-313085!, P [barcode] P00468554!, P [barcode] P00468555!, P [barcode] P00468556!).

Nomenclatural note. Three syntypes were cited in the protologue for this species, *Claussen 197*, *Claussen 422* (G-DC!), and *Claussen 507* (G!, G as photo F neg. 7665 at MO-1692780!). In addition, a Claussen specimen located at MO (MO-2245221!) seems to correspond to one of these collections but has no collection number. The collection *Claussen 197* is the most widely distributed and is here designated as the type; the specimen at G-DC is chosen as the lectotype because it was available to de Candolle.

Habitat and distribution. This species is found in dry forest vegetation in eastern Brazil (Bahia, Minas Gerais).

12. Fridericia conjugata (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia conjugata* Vell., Fl. Flumin. 231. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 18. 1827 [1831]. *Arrabidaea conjugata* (Vell.) Mart., Flora 24(2, Beibl.): 46. 1841. *Fridericia conjugata* (Vell.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1605. 2008, nom. nud. invalid. *Fridericia conjugata* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: tab. 18 in Vellozo, Fl. Flumin., Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found widely in humid forest vegetation in Guatemala, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Caquetá, César, Chocó, Magdalena, Santander, Sucre, Vichada), Venezuela (Falcón), French Guiana, Ecuador, Peru (Huánuco, Madre de Dios), Bolivia, Brazil (Acre, Amapá, Amazonas, Bahia, Distrito Federal, Espírito Santo, Maranhão, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia, São Paulo, Sergipe), and Argentina (Misiones).

13. Fridericia corchoroides (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia corchoroides* Cham., Linnaea 7: 706. 1832 [1833]. *Arrabidaea corchoroides* (Cham.) DC., in A. DC., Prodr. 9: 183. 1845. *Fridericia corchoroides* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., Nov., *F. Sellow 1603* (holotype, LE not seen; isotype, B†, B as photo F neg. 18448 at K! and at MO-1692782!, US-2825544 image!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Minas Gerais, Piauí, São Paulo).

14. Fridericia costaricensis (Kraenzl.) L. G. Lohmann, comb. nov. Basionym: *Saldanhaea costaricensis* Kraenzl., Repert. Spec. Nov. Regni Veg. 17(8–12): 124. 1921. *Arrabidaea costaricensis* (Kraenzl.) A. H. Gentry, Brittonia 25(3): 231. 1973. TYPE: Costa Rica. Puntarenas: Nicoya, May 1900, *A. Tonduz 13929* (holotype, B†; lectotype, designated here, G not seen, G as photo F neg. 26204 at MO-1693049!; isolectotypes, F-1012279 image!, K [barcode] K000449474 image!, MO-2229714!, MO-3401780!, US-861250 image!, US-862811 image!, US-861250 and US-862811 together as unnumbered photo at MO-1130237!).

Nomenclatural note. The best material and part of the principal set of Tonduz's materials of this

species are deposited in Geneva, and the G specimen is here selected as the lectotype.

Habitat and distribution. This species is found in dry forest vegetation in Mexico (Chiapas, Oaxaca), Honduras, Nicaragua, and Costa Rica.

15. Fridericia crassa (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Distictis crassa* Bureau & K. Schum., Fl. Bras. 8(2): 177. 1896. *Arrabidaea crassa* (Bureau & K. Schum.) Sprague, Hooker's Icon. Pl. 30: tab. 2933. 1911. *Distictella crassa* (Bureau & K. Schum.) Urb., Repert. Spec. Nov. Regni Veg. 14: 310. 1916. *Fridericia crassa* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Piauí: Oeiras, 1840, *G. Gardner 2468* (lectotype, designated here, P [barcode] P00468562!, P [barcode] P00468562 as photocopy at MO-2692718!; isolectotypes, P [barcode] P00468563!, P [barcode] P00468564!, P [barcode] P00468565!, W!, W as photo F neg. 32862 at MO-1692953!).

Nomenclatural note. Original material of the type collection is at P where Bureau worked. Four duplicates are deposited there, and the specimen with the best material is here selected as the lectotype.

Habitat and distribution. This species is found in dry forest vegetation in northeastern Brazil (Maranhão).

16. Fridericia craterophora (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia craterophora* DC., in A. DC., Prodr. 9: 147. 1845. *Arrabidaea craterophora* (DC.) Bureau, Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 6, 6(3): 422. 1892. *Fridericia craterophora* (DC.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1605. 2008, nom. nud. invalid. *Fridericia craterophora* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: betw. Serro Frio & Contendas, s.d., *C. F. P. von Martius 33* (holotype, M!; isotype, P [barcode] P00468566!).

Habitat and distribution. This species is found in dry forest and cerrado vegetation in eastern Bolivia, Paraguay, and Brazil (Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, São Paulo).

17. Fridericia cuneifolia (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia cuneifolia* DC., in A. DC., Prodr. 9: 157. 1845. *Petastoma cuneifolium* (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 77. 1896. *Arrabidaea cuneifolia* (DC.) Sandwith, Kew Bull. 22: 413. 1968. *Fridericia cuneifolia* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: Serro Frio, *C. F. P. von Martius 337* (holotype, G-DC not seen; isotype, M-86375!, M-86375 as unnumbered photo at MO-1693016!).

Habitat and distribution. This species is found in cerrado and dry caatinga vegetation in eastern Brazil (Bahia, Minas Gerais, Piauí).

18. Fridericia dichotoma (Jacq.) L. G. Lohmann, comb. nov. Basionym: *Bignonia dichotoma* Jacq., Enum. Syst. Pl. 25. 1760, non *Arrabidaea dichotoma* Bureau, 1893. *Panterpa dichotoma* (Jacq.) Miers, Proc. Roy. Hort. Soc. London 3: 196. 1863. *Fridericia dichotoma* (Jacq.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1605. 2008, nom. nud. invalid. *Fridericia dichotoma* (Jacq.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Colombia. Magdalena: Cartagena, not located.

Bignonia corallina Jacq., Fragm. Bot. 37, tab. 42, fig. 1. 1809. *Arrabidaea corallina* (Jacq.) Sandwith, Bull. Misc. Inform. Kew 8(4): 460. 1953 [1954]. TYPE: Venezuela. Caracas, s.d., *N. J. Jacquin s.n.* (holotype, W not seen, W as photo F neg. 32859 at MO-1692933!).

Nomenclatural note. *Bignonia dichotoma* is the oldest name for this species (Sandwith, 1954a: 460) and the corresponding combination is made here in *Fridericia*. However, that particular name has not been used for this species recently, because this species was included in *Arrabidaea* where the name *A. dichotoma* Bureau was previously published for a different species (here called *Tanaecium selloi* (Spreng.) L. G. Lohmann). In *Arrabidaea* this species is correctly called *A. corallina* (Jacq.) Sandwith.

Gentry (1977) suggested that Jacquin's specimen at W that is labeled as being from Caracas, Venezuela, and identified as *Bignonia corallina* may also be the type material of *B. dichotoma*, but he did not explain the situation or his reasoning further. No information was given in the protologue about where *B. dichotoma* was found, though in a later work (Jacquin, 1763) the type locality of *B. dichotoma* was reported as Cartagena, Colombia, where Jacquin did collect. No original material that can be clearly connected with the name *B. dichotoma* has been traced so far nor has this species been directly connected in Jacquin's works with *B.*

corallina, so further studies are needed before the typification of this name can be resolved.

Habitat and distribution. This species is widely and commonly found in dry to humid lowland forest vegetation in Mexico (Chiapas, Colima, Guerrero, Jalisco, México, Oaxaca, Veracruz), Belize, Guatemala, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Atlántico, Bolívar, César, Chocó, Huila, La Guajira, Magdalena, Meta, Sucre, Tolima), Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia), Guyana, Suriname, French Guiana, Ecuador, Peru (Cusco, Loreto, Madre de Dios, Piura, San Martín, Tumbes, Ucayali), Bolivia, Paraguay, Brazil (Acre, Alagoas, Amapá, Amazonas, Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo, Tocantins), and Argentina (Chaco, Corrientes, Formosa, Jujuy, Misiones, Salta).

19. Fridericia dispar (Bureau ex K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea dispar* Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Fridericia dispar* (Bureau ex K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: near Japira, Dec. 1840, *J. S. Blanchet 3082* (lectotype, designated here, NY [barcode] NY00313088!, NY [barcode] NY00313088 as photocopy at MO-1692785!; isolectotypes, BR-879951!, BR-879934!, G-DC not seen, G-DC as photo F neg. 7630 at MO-1692785!, US-2515208 image!).

Nomenclatural note. No specimens were cited in the protologue of this species, where the name was attributed to Bureau. Bureau and Schumann (1896) in a contemporaneous treatment cited three specimens of *Arrabidaea dispar* from Bahia, which can be considered original material: *Blanchet 3082*, *Martius s.n.* from near Maracão, and *Glaziou 11226*, for which the collection locality is unknown. The Blanchet collection was the only one located and is here chosen as the type of this species; the specimen at NY is designated the lectotype because it is in the best condition and the only specimen that includes flowers.

Habitat and distribution. This species is found in dry forest, cerrado, and caatinga vegetation in northeastern Brazil (Bahia, Ceará, Maranhão, Pará, Paraíba, Pernambuco).

20. Fridericia egensis (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea egensis* Bureau & K. Schum., Fl. Bras. 8(2): 65. 1896. *Fridericia egensis* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Alto Amazonas, betw. Tefé & Ega, Dec. 1821, *E. F. Poeppig 2895* (lectotype, designated here, W!, W as photo F neg. 32855 at MO-1692870!; isolectotypes, K!, W!).

Nomenclatural note. Two adequate duplicates of the type collection are deposited at W in Poeppig's original materials, and were annotated by him with this name. One of these was photographed by the Field Museum with the photos widely distributed, and this is chosen here as the lectotype.

Habitat and distribution. This species is found in wet forest vegetation in Venezuela (Amazonas), Guyana, Ecuador, Peru (Loreto), Bolivia, and Brazil (Amazonas, Maranhão, Pará).

21. Fridericia elegans (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia elegans* Vell., Fl. Flumin. 247. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 27. 1827 [1831]. *Adenocalymma elegans* (Vell.) Mart. ex K. Schum., Nat. Pflanzenfam. 4(3b): 214. 1894. *Pseudocalymma elegans* (Vell.) Kuhlm., Rodriguésia 5(14): 365. 1941. *Arrabidaea elegans* (Vell.) A. H. Gentry, Taxon 24(4): 338. 1975. *Fridericia elegans* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: tab. 27 in Vellozo, Fl. Flumin., Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Rio de Janeiro).

22. Fridericia erubescens (DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia erubescens* DC., in A. DC., Prodr. 9: 157. 1845. *Cuspidaria erubescens* (DC.) Bureau, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 1893: 102. 1893 [1894]. *Piriadacus erubescens* (DC.) Pichon, Bull. Soc. Bot. France 92: 225. 1946. *Alsocydia erubescens* (DC.) J. C. Gomes, Revista Brasil. Biol. 11: 49. 1951. *Fridericia erubescens* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: Serro Frio, July 1818, *C. F. P. von Martius s.n.* (lectotype, designated here, M-88919!, M-88919 as photo K neg. 59450 at K!; isolectotypes, M-88918!, M-88918 as photo K

neg. 5944 at K!, M-88920!, M-88920 as photo K neg. 5947 at K!).

Nomenclatural note. The name *Cuspidaria erubescens* as first used by Bureau (1864: 5, tab. 3) was apparently not intended to describe a new species, but to transfer the name *Bignonia erubescens* to *Cuspidaria*. However, Bureau made no reference there to this basionym, and thus the name was not validly published there and only validated later in a more complete publication. No collection number was listed in the protologue of *B. erubescens* for the Martius collection that was cited. A set of unnumbered Martius collections deposited at M that match the locality described by de Candolle and whose identity corresponds to this species are here chosen as the type, and the best material deposited is here selected as the lectotype.

Habitat and distribution. This species is found in cerrado and dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Pernambuco, Piauí, Rio de Janeiro).

23. Fridericia fagoides (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia fagoides* Cham., Linnaea 7: 680. 1832 [1833]. *Arrabidaea fagoides* (Cham.) Bureau, in J. E. B. Warming, Lagoa Santa 270. 1892. *Fridericia fagoides* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1605. 2008, nom. nud. invalid. *Fridericia fagoides* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *F. Sellow 1602* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18450 at MO-1692786!, NY [barcode] NY00579081!, NY [barcode] NY00579081 as photocopy at MO-2927267!).

Habitat and distribution. This species is found in dry forest vegetation in Bolivia, Paraguay, and Brazil (Espírito Santo, Goiás, Mato Grosso do Sul, Minas Gerais, Rio de Janeiro).

24. Fridericia fanshawei (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea fanshawei* Sandwith, Bull. Torrey Bot. Club 75: 662. 1948. *Fridericia fanshawei* (Sandwith) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: British Guiana [Guyana]. Mazaruni River, 24 Jan. 1944, *D. B. Fanshawe 4288* (holotype, K!; isotype, NY [barcode] NY00313090!).

Habitat and distribution. This species is found in wet forest vegetation in South America, in Colombia (Amazonas), Venezuela (Bolívar, Delta Amacuro), Guyana, French Guiana, and Suriname to Ecuador, Peru (Amazonas, Loreto, Madre de Dios, Pasco, San Martín), Bolivia, and Brazil (Amapá, Amazonas, Mato Grosso, Pará).

25. Fridericia floribunda (Kunth) L. G. Lohmann, comb. nov. Basionym: *Bignonia floribunda* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 134. 1818 [1819]. *Arrabidaea floribunda* (Kunth) Loes., Repert. Spec. Nov. Regni Veg. 16: 209. 1919. TYPE: Mexico. Campeche: s. loc., s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P-Bonpl.!).

Habitat and distribution. This species is found in dry lowland forest vegetation in Mexico (Campeche, Chiapas, Guerrero, Michoacán, Oaxaca, Quintana Roo, Veracruz, Yucatán), Belize, Guatemala, El Salvador, and Panama.

26. Fridericia florida (DC.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea florida* DC., in A. DC., Prodr. 9: 184. 1845. *Fridericia florida* (DC.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1605. 2008, nom. nud. invalid. *Fridericia florida* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Rio Negro, Japurá, Dec. 1819, *C. F. P. von Martius s.n.* (lectotype, designated here, M-86371!; isolectotypes, G-DC!, G-DC as photo F neg. 7669 at MO-1692787!, K [barcode] K000402519!, M-86370!, M-86367!, M-86368!, M-86369!).

Nomenclatural note. No collection number was given in the protologue for the Martius collection that was cited. A set of unnumbered Martius collections that match the locality described by de Candolle and whose identity corresponds to this species are here chosen as the type, and the best quality specimen at M is selected as lectotype.

Habitat and distribution. This species is widely and commonly found in dry to humid, lowland to premontane forest vegetation in Mexico (Campeche, Chiapas, Oaxaca, Tabasco, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Boyacá, Caldas, Caquetá, Chocó, Córdoba, La Guajira, Magdalena, Meta, Putumayo, Risaralda, Santander, Tolima, Vaupés), Venezuela (Amazonas, Apure, Bolívar, Carabobo, Cojedes, Distrito Federal, Mérida, Miranda, Portuguesa, Sucre, Táchira, Zulia), Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Junín,

Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, Paraguay, Brazil (Acre, Amapá, Amazonas, Bahia, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Rio de Janeiro, Rondônia, Roraima, São Paulo), and Argentina (Misiones).

27. Fridericia formosa (Bureau) L. G. Lohmann, comb. nov. Basionym: *Petastoma formosum* Bureau, Rev. Hort. 40: 154. 1868, nom. nud., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 100. 1894. *Petastoma formosa*, orth. var. *Arrabidaea formosa* (Bureau) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia formosa* (Bureau) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: close to Ayuruaca near Rio Preto, 18 Apr. 1878, *A. Glaziou 9526* (lectotype, designated here, P [barcode] P00608051!; isolectotype, P [barcode] P00608052!).

Nomenclatural note. There has been confusion about the place of publication of this name. Bureau first mentioned it in the *Revue Horticole* but provided no diagnosis, thus that name was not validly published there. This name was later cited as newly published in the Flora Brasiliensis (Bureau & Schumann, 1896), but in fact it was validly described prior to that. In the actual protologue three syntypes from Brazil are listed: *Warming s.n.* from Lagoa Santa in Minas Gerais, *Glaziou 9526* from Ayuruaca in Minas Gerais, and *Glaziou 16266* from an unknown locality. (Additional specimens were cited in the Flora Brasiliensis, but these do not constitute syntypes in this case.) Of the syntypes examined, the specimens of *Glaziou 9526* deposited at P are most likely to represent original material and also have the best material and locality information; therefore, this collection is chosen as the type. There is one sheet of this collection at P with flowers and another with fruits; the flowering specimen is selected here as the lectotype because the flowers are diagnostic for this species.

Habitat and distribution. This species is found in cerrado and deciduous forest vegetation in southeastern Brazil (Distrito Federal, Minas Gerais, São Paulo).

28. Fridericia grosourdyana (Baill.) L. G. Lohmann, comb. nov. Basionym: *Paramansoa grosourdyana* Baill., Hist. Pl. 10: 27. 1888. *Arrabidaea grosourdyana* (Baill.) Sandwith, Kew Bull. 22: 418. 1968. TYPE: Venezuela. Bolívar: Villa de Upata, 1864, *R. de Grosourdy s.n.* (lectotype, designated here, P [barcode] P00468560!; isolectotype, P [barcode] P00468561!).

Nomenclatural note. No collection number was listed in the protologue for the Grosourdy collection that was cited. A set of unnumbered Grosourdy collections at P that match the locality described by Baillon and whose identity corresponds to this species are here chosen as the type, and the best quality material is selected as lectotype.

Habitat and distribution. This species is found in wet lowland to premontane forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Bolívar), Guyana, and French Guiana.

29. Fridericia japurensis (DC.) L. G. Lohmann, comb. nov. Basionym: *Tabebuia japurensis* DC., in A. DC., Prodr. 9: 214. 1845. *Macfadyena japurensis* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 200. 1863. *Arrabidaea japurensis* (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 65. 1896. *Scobinaria japurensis* (DC.) Sandwith, Kew Bull. 13: 440. 1858 [1859]. *Fridericia japurensis* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Rio Negro, Japurá, Dec. 1819, *C. F. P. von Martius 182* (holotype, G-DC!; isotype, M-86354!, M-86354 as photo F neg. 20439 at K! and at MO-1692789!).

Habitat and distribution. This species is widely found in evergreen lowland forest vegetation (Gentry, 1997) in Belize, Nicaragua, Panama, Colombia (Amazonas, Bolívar, Caquetá, Vaupés), Venezuela (Amazonas, Bolívar, Delta Amacuro), Suriname, French Guiana, Ecuador, Peru (Amazonas, Loreto, Madre de Dios, Pasco), Bolivia, and Brazil (Acre, Amapá, Amazonas, Mato Grosso, Minas Gerais, Pará, Roraima).

30. Fridericia lauta (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea lauta* Bureau & K. Schum., Fl. Bras. 8(2): 43. 1896. *Pyrostegia lauta* Miers, Proc. Roy Hort. Soc. 3: 188. 1863, nom. nud. *Fridericia lauta* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Pará: Santarém, May 1850, *R. Spruce 716* (lectotype, designated here, K [barcode] K000449130!; isolectotypes, K [barcode] K000449131!, M-88926!, M-88926 as photo F neg. 20440 at MO-1692790!, W!, W as photo F neg. 32857 at MO-1692878!).

Nomenclatural note. Miers's specimens are presumably at BM (Stafleu & Cowan, 1981), but no

material of the type collection was found there or at P, where Bureau worked. Spruce's main set of collection is at K, where there are two sheets; the best of these is here chosen as the lectotype.

Habitat and distribution. This species is found in seasonal and dry vegetation in Amazonian Brazil (Acre, Amazonas, Pará, Rondônia).

31. Fridericia leucopogon (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia leucopogon* Cham., Linnaea 7: 707. 1832 [1833]. *Panterpa leucopogon* (Cham.) Miers, Proc. Roy. Hort. Soc. 3: 196. 1863. *Petastoma leucopogon* (Cham.) Bureau ex Warm., Symbolae 40: 1215. 1893. *Arrabidaea leucopogon* (Cham.) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia leucopogon* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard, 107(2): 1605. 2008, nom. nud. invalid. *Fridericia leucopogon* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (holotype, LE not seen; isotype, G-DC!).

Habitat and distribution. This species is found in dry to moist forest vegetation in Bolivia and Brazil (Bahia, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pernambuco, Rio de Janeiro, Santa Catarina, São Paulo).

32. Fridericia limae (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea limae* A. H. Gentry, Phytologia 46(4): 204. 1980. *Fridericia limae* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Pernambuco: 6 km Espírito Santo [sic], on rd. to Araripina, 4 Jan. 1961, *A. Lima 61–3592* (holotype, INPA-13239 not seen, INPA-13239 as photocopy at MO-2698845!; isotype, MO-2630121!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Pernambuco, Piauí).

33. Fridericia mollis (Vahl) L. G. Lohmann, comb. nov. Basionym: *Bignonia mollis* Vahl, Eclog. Amer. 2: 46. 1798. *Arrabidaea mollis* (Vahl) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Fridericia mollis* (Vahl) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: French Guiana. s. loc., s.d., *J. P. von Rohr s.n.* (holotype, C not seen, C as photo F neg. 22150 at MO-1692792!).

Habitat and distribution. This species is found in wet lowland to premontane forest vegetation (Gentry, 1997) in Venezuela (Bolívar, Delta Amacuro), Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Pará, Roraima).

34. Fridericia mollissima (Kunth) L. G. Lohmann, comb. nov. Basionym: *Bignonia mollissima* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 133. 1818 [1819]. *Panterpa mollissima* (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 196. 1863. *Arrabidaea mollissima* (Kunth) Bureau & K. Schum., Fl. Bras. 8(2): 46. 1896. TYPE: Venezuela. Aragua: Caracas, Valles de Aragua, Villa de Cura, Mar., *F. W. H. A. von Humboldt & A. J. A. Bonpland 740* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39422 at MO-1692928!; isotype, B-W-11431!).

Nomenclatural note. The names *Bignonia mollissima* Kunth and *B. littoralis* Kunth were published simultaneously; these have long been synonymized under the name *B. mollissima* (e.g., Gentry, 1973b).

Habitat and distribution. This species is found in semideciduous forest vegetation (Gentry, 1997) in Mexico (Chiapas, Guerrero, Oaxaca, Veracruz), the Greater Antilles (Jamaica), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Atlántico, Bolívar, César, Chocó, Córdoba, Cundinamarca, Magdalena, Sucre), Venezuela (Anzoátegui, Apure, Aragua, Bolívar, Carabobo, Distrito Federal, Falcón, Guárico, Lara, Miranda, Portuguesa, Sucre, Zulia).

35. Fridericia monophylla (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea monophylla* A. H. Gentry, Mem. New York Bot. Gard. 29: 274. 1978. *Fridericia monophylla* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. Roraima: Rio Anauá, tributary of Rio Branco, 30 Apr. 1974, *J. Murça-Pires, P. B. Cavalcante, H. Magnano & N. T. Silva 14491* (holotype, IAN not seen; isotype, MO-2232884!).

Habitat and distribution. This species is found in campinas vegetation on white sand substrates in northern Brazil (Amazonas, Pará, Roraima).

36. Fridericia nicotianiflora (Kraenzl.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea nicotianiflora* Kraenzl., Notizbl. Bot. Gart. Berlin-Dahlem 6: 369. 1915, as "*nicotianaeflora*." *Fridericia nicotianiflora* (Kraenzl.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010,

nom. nud. invalid. TYPE: Brazil. Acre: Rio Branco, Seringal São Francisco, Apr. 1911, *E. Ule 9782* (holotype, B†, B as photo F neg. 18451 at MO-1692795!; lectotype, designated here, K [barcode] K000403352!).

Nomenclatural note. The only isotype located during this study is here chosen as the lectotype, to replace the destroyed holotype.

Habitat and distribution. This species is found in seasonal vegetation in Colombia (Córdoba, Putumayo), Ecuador, Peru (Huánuco, Madre de Dios, Puno), Bolivia, and western Brazil (Acre, Rondônia).

37. Fridericia nigrescens (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea nigrescens* Sandwith, Lloydia 2: 209. 1939. *Fridericia nigrescens* (Sandwith) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Amapá: close to border with Guyana, Akarai Mtns., height of land betw. drainage of River Mapuera (Trombetas tributary) & Shodikar Creek (Essequibo tributary), 600–800 m, 19 Jan. 1938, *A. C. Smith 2977* (holotype, F-1023607!; isotypes, G-8849! K!, MO-1165475!, NY [barcode] NY00313104!, P [barcode] P00468547!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Guainía), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Peru (Madre de Dios), Bolivia, and Brazil (Acre, Amapá, Amazonas, Maranhão, Pará, Rondônia).

38. Fridericia oligantha (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea oligantha* Bureau & K. Schum., Fl. Bras. 8(2): 63. 1896. *Fridericia oligantha* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. s. loc., s.d., *G. Gardner 1258* (holotype, W!, W in photo F neg. 32858 at MO-1692874!).

Habitat and distribution. This species is found in humid vegetation in Colombia (Amazonas), Ecuador, Guyana, Suriname, French Guiana, and Brazil (Acre, Maranhão, Pará).

39. Fridericia ornithophila (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea ornithophila* A. H. Gentry, Ann. Missouri Bot. Gard. 64: 312, fig. 1. 1977 [1978]. *Fridericia ornithophila* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Pará: Acará, Thomé Açú, Pão Vermelho, 3 Aug. 1931, *Y. Mexia 6041* (holotype, MO-1068874!; isotypes, NY [barcode] NY00346064!, US-1615868 image!).

Habitat and distribution. This species is found in wet forest vegetation in northern Bolivia and Brazil (Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia).

40. Fridericia oxycarpa (Urb.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea oxycarpa* Urb., Repert. Spec. Nov. Regni Veg. 14: 301. 1916. TYPE: Trinidad. Close to Moruga, June, *W. E. Broadway 3188* (holotype, B†).

Nomenclatural note. No duplicates of the type have been located at NY, but herbaria in Trinidad where a duplicate might be deposited have not been searched yet. Therefore the typification of this species cannot yet be clarified.

Habitat and distribution. This species is found in semideciduous forest vegetation (Gentry, 1997) in Panama, Colombia (Bolívar, Cundinamarca, Magdalena), Venezuela (Amazonas, Anzoátegui, Bolívar, Cojedes, Guárico, Lara, Miranda, Portuguesa, Sucre, Zulia), Trinidad and Tobago, and Brazil (Amazonas).

41. Fridericia paradoxa (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Petastoma paradoxum* Sandwith, Kew Bull. 9: 603. 1954 [1955]. *Arrabidaea paradoxa* (Sandwith) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia paradoxa* (Sandwith) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: near Tamabury, Oct. 1906, *E. Ule 7067* (holotype, K!, K as photocopy at MO-2904335!; isotypes, B [barcode] B100186001!, B [barcode] B100186001 as photocopy at MO-2719406!, HBG not seen).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Piauí).

42. Fridericia parviflora (Mart. ex DC.) L. G. Lohmann, comb. nov. Basionym: *Pithecoctenium parviflorum* Mart. ex DC., in A. DC., Prodr. 9: 197. 1845. *Arrabidaea parviflora* (Mart. ex DC.) Bureau & K. Schum., Fl. Bras. 8(2): 53. 1896. *Fridericia parviflora* (Mart. ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Rio de Contas, Oct. 1818, *C. F. P. von Martius s.n.* (lectotype, designated here, M-86353!, M-86353 in photo F neg. 20441 at MO-1692849!).

Nomenclatural note. No collection number was given for the Martius collection that was cited in the protologue of this species. An unnumbered Martius collection of this species at M corresponds to the type locality and is here designated as the lectotype. Gentry noted in sched. that there is a label mix-up on two photos, F neg. 20441 and F. neg. 20442. F neg. 20441 is labeled "Arrabidaea plicifolia" but actually corresponds to the type of *Pithecoctenium parviflorum* (≡ *Fridericia parviflora*), while F neg. 20442 is labeled "Arrabidaea parviflora" but actually corresponds to the type of *Adenocalymma plicifolium* Mart. ex DC. [≡ *F. pliciflora* (Mart. ex DC.) L. G. Lohmann].

Habitat and distribution. This species is found in dry forest vegetation in southern and eastern Brazil (Bahia, Ceará, Mato Grosso do Sul, Minas Gerais, Paraíba, Pernambuco).

43. Fridericia patellifera (Schltdl.) L. G. Lohmann, comb. nov. Basionym: *Bignonia patellifera* Schltdl., Linnaea 8: 516. 1833. *Petastoma patelliferum* (Schltdl.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Arrabidaea patellifera* (Schltdl.) Sandwith, Kew Bull. 22: 413. 1968. *Fridericia patellifera* (Schltdl.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Mexico. Veracruz: prope la Hacienda de la Laguna, *C. J. W. Schiede 153* (holotype, HAL not seen; isotypes, MO-2005562!, P [barcode] P00468579!).

Habitat and distribution. This species is widely and commonly found in dry to humid, lowland to premontane forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Colima, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, Quintana Roo, Tabasco, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Boyacá, Caquetá, César, Chocó, Magdalena, Meta, Nariño, Santander), Venezuela (Amazonas, Bolívar, Falcón, Mérida, Miranda, Táchira, Yaracuy, Zulia), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Espírito Santo, Mato Grosso, Pará, Rondônia, Roraima).

44. Fridericia pearcei (Rusby) L. G. Lohmann, comb. nov. Basionym: *Bignonia pearcei* Rusby, Mem. Torrey Bot. Club 6: 100. 1906. *Arrabidaea pearcei* (Rusby) K. Schum. ex Urb., Repert. Spec. Nov. Regni Veg. 14: 302. 1914. *Fridericia pearcei* (Rusby) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Bolivia. La Paz: Guanai-Tipuani, Apr.–June 1892, *A. M. Bang 1391* (holotype, NY-313146!; isotypes, F-163739 image!, G-9126!, G-9125!, M-86363!, MO-2005581!, US-47714 image!, US-47713 image!, US-1322423 image!).

Habitat and distribution. This species is found in wet forest vegetation in Colombia (La Guajira), Ecuador, Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), and Brazil (Amazonas, Pará).

45. Fridericia platyphylla (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia platyphylla* Cham., Linnaea 7: 679. 1832. *Bignonia brachypoda* DC., in A. DC., Prodr. 9: 146. 1845, nom. illeg. superfl. *Arrabidaea brachypoda* Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 98, 1894, replacement name, non *Arrabidaea platyphylla* DC., 1845. *Arrabidaea platyphylla* (Cham.) Bureau & K. Schum., Fl. Bras. 8(2): 38. 1896, hom. illeg., non *Arrabidaea platyphylla* DC., 1845. *Bignonia brachypoda* var. *platyphylla* (Cham.) DC., in A. DC., Prodr. 9: 146. 1845. *Fridericia platyphylla* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia platyphylla* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. San Antonio do Monte, s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18452 at MO-1692775!, HAL-098686 image!, K [barcode] K000449124 image!, US-282538 image!).

Nomenclatural note. The name *Bignonia brachypoda* DC. was illegitimate when it was published because the previously published valid name *B. platyphylla* Cham. was included within the circumscription of the species as a synonym, but that name should have been used for this species instead. De Candolle did not designate a type for his species, and named several varieties but did not indicate which of them was the typical variety. Therefore his name *B. brachypoda* is a superfluous name that is typified by the type of the name that should correctly have been adopted, *B. platyphylla* (McNeill et al., 2006, Art. 52.2). Later Bureau intended to transfer the illegitimate name *B. brachypoda* into *Arrabidaea* because he thought it was the correct name for this species, but Bureau's name is not a legitimate combination because his intended basionym is illegitimate. However, Bureau's name does represent a legitimate, valid replacement name for the name *B. brachypoda*, which was needed because the name *A. platyphylla*

was previously published for a different species and thus cannot be used for this species. Shortly after Bureau's replacement name was published, Bureau and Schumann (1896) noticed that the name *B. platyphylla* was the older name for this species and accordingly transferred that name into *Arrabidaea*; however, their intended new combination here is illegitimate because, as noted, the name *A. platyphylla* had previously been published for another species.

Habitat and distribution. This species is found in seasonal and cerrado vegetation in Venezuela (Amazonas, Bolívar, Carabobo, Cojedes, Delta Amacuro, Guárico, Portuguesa), Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, Paraguay, and Brazil (Acre, Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Piauí, Rio de Janeiro, Rondônia, Roraima, São Paulo, Tocantins).

46. Fridericia pliciflora (Mart. ex DC) L. G. Lohmann, comb. nov. Basionym: *Adenocalymma pliciflorum* Mart. ex DC., in A. DC., Prodr. 9: 202. 1845. *Arrabidaea pliciflora* (Mart. ex DC.) Bureau & K. Schum., Fl. Bras. 8(2): 51. 1896. *Fridericia pliciflora* (Mart. ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Piauí: s. loc., Mar. 1818, *C. F. P. von Martius 1874* (holotype, M-86392!, M-86392 as photo F neg. 20442 at MO-1692846!; isotype, G-DC!).

Nomenclatural note. Gentry noted in sched. that there is a label mix-up on two photos, F neg. 20441 and F. neg. 20442: F neg. 20441 is labeled "Arrabidaea plicifolia" but actually corresponds to the type of *Pithecoctenium parviflorum* (≡ *Fridericia parviflora*), while F neg. 20442 is labeled "Arrabidaea parviflora" but actually corresponds to the type of *Adenocalymma plicifolium* (≡ *F. pliciflora*).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Ceará, Maranhão, Piauí).

47. Fridericia podopogon (DC.) L. G. Lohmann, comb. nov. Basionym: *Spathodea podopogon* DC., in A. DC., Prodr. 9: 205. 1845. *Macfadyena podopogon* (DC.) Griseb., Cat. Pl. Cub. 195. 1866. *Neomacfadya podopogon* (DC.) Baill. ex K. Schum., Nat. Pflanzenfam. 4(3b): 227. 1984 (as "*Neomacfadyena*"). *Arrabidaea podopogon* (DC.) A. H. Gentry, Rhodora 79: 439. 1977. TYPE: Cuba. Havana, 1829, *R. de la Sagra 293* (holotype, G-DC!, G-DC in photo F neg. 33894 at MO-1693063!).

Habitat and distribution. This species is found in dry forest vegetation in Mexico (Campeche, Oaxaca, Quintana Roo, Yucatán), the Greater Antilles (Cuba), Belize, and Guatemala.

48. Fridericia poeppigii (DC.) L. G. Lohmann, comb. nov. Basionym: *Anemopaegma poeppigii* DC., in A. DC., Prodr. 9: 190. 1845. *Petastoma poeppigii* (DC.) Sandwith, Candollea 7: 249. 1937. *Arrabidaea poeppigii* (DC.) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia poeppigii* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Peru. s. loc., 1832, *E. F. Poeppig 75* (holotype, G-DC!, G-DC in photo F neg. 7661 at MO-1692746!).

Habitat and distribution. This species is found in dry seasonal and cerrado vegetation in Peru (Cusco, Madre de Dios), Bolivia, and Brazil (Distrito Federal, Goiás, Minas Gerais, São Paulo).

49. Fridericia prancei (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea prancei* A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 50, fig. 1A. 1976. *Fridericia prancei* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Km. 67 E of Manaus–Itacoatiara Rd., 24 Nov. 1974, *A. H. Gentry 12822* (holotype, INPA!; isotypes, MO-2251712!, RB-185813 [barcode] 53870!, RB-185813 [barcode] 538142!, RB-185813 [barcode] 538143!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas), Venezuela (Amazonas), Peru (Puno), and Brazil (Acre, Amazonas, Pará, Rondônia).

50. Fridericia pubescens (L.) L. G. Lohmann, comb. nov. Basionym: *Bignonia pubescens* L., Sp. Pl. (ed. 2) 2: 870. 1763. *Petastoma pubescens* (L.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Arrabidaea pubescens* (L.) A. H. Gentry, Brittonia 25(3): 239. 1973. *Fridericia pubescens* (L.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia pubescens* (L.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Mexico. Campeche, s.d., *W. Houston s.n.* (holotype, LINN-776.3 fiche!; isotype, BM!).

Habitat and distribution. This species is widely and commonly found in dry to humid forest vegetation in Mexico (Campeche, Chiapas, Colima, Oaxaca, Querétaro, Quintana Roo, San Luis Potosí, Tabasco, Tamaulipas, Veracruz, Yucatán), Belize, Guatemala, Panama, Colombia (Atlántico, Bolívar, César, Cundinamarca, Huila, Magdalena, Meta, Sucre, Vichada), Venezuela (Amazonas, Anzoáteguí, Aragua, Barinas, Bolívar, Carabobo, Distrito Federal, Falcón, Guárico, Lara, Miranda, Monagas, Portuguesa, Sucre, Táchira, Zulia), Trinidad and Tobago, Guyana, Suriname, Ecuador, Peru (Loreto, Madre de Dios, San Martín, Tumbes, Ucayali), Bolivia, Paraguay, and Brazil (Acre, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Minas Gerais, Pará, Paraíba, Pernambuco, Rio de Janeiro, Roraima, São Paulo, Sergipe).

51. Fridericia rego (Vell.) L. G. Lohmann, comb. nov. Basionym: *Bignonia rego* Vell., Fl. Flumin. 249. 1825 [1829], as "*rego*"; Fl. Flumin. Icon. 6: tab. 39. 1827 (1831), as "*sego*." *Arrabidaea rego* (Vell.) DC., Biblioth. Univers. Geneve, sér. 2. 17: 126. 1838. *Vasconcellia rego* (Vell.) Mart., Flora 24(2, Beibl.): 12. 1841, as "*sego*." *Chasmia rego* (Vell.) Kuntze, Revis. Gen. Pl. 2: 479. 1891. *Fridericia rego* (Vell.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: tab. 39 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in humid to dry forest vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Paraíba, Rio de Janeiro, São Paulo).

52. Fridericia samydoides (Cham.) L. G. Lohmann, comb. nov. Basionym: *Bignonia samydoides* Cham., Linnaea 7: 669. 1832 [1833]. *Petastoma samydoides* (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Arrabidaea samydoides* (Cham.) Sandwith, Kew Bull. 22: 413. 1968. *Fridericia samydoides* (Cham.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia samydoides* (Cham.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. São Paulo: s. loc., s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, B in photo F neg. 18490 at MO-1692906!, G-DC!, NY-111536!, P [barcode] P00468580!, P [barcode] P00468581!).

Nomenclatural note. The B specimen cited here is labeled as collected by Sellow, without a collection number. Another specimen of this species at B is labeled as *Sellow 5243* and was also photographed as a possible type of this name (F neg. 18489 at MO-1692905!), but seems to be a different collection.

Habitat and distribution. This species is found in cerrado vegetation in Paraguay, southeastern Brazil (Espírito Santo, Minas Gerais, Paraná, Santa Catarina, São Paulo), and northern Argentina (Misiones).

53. Fridericia schumanniana (Loes.) L. G. Lohmann, comb. nov. Basionym: *Paragonia schumanniana* Loes., Bot. Jahrb. Syst. 23: 130. 1896, non *Arrabidaea schumanniana* Huber, 1906. TYPE: Nicaragua. Matagalpa: near Cañada Yasica, ca. 800 m, Aug., *E. Rothschuh 230* (holotype, B†).

Adenocalymma verrucosum Standl., Publ. Field Columbian Mus., Bot. Ser. 4: 323. 1929. *Martinella verrucosa* (Standl.) Standl., Contr. Arnold Arbor. 5: 138. 1933. *Scobinaria verrucosa* (Standl.) Seibert, Publ. Carnegie Inst. Wash. 522: 408. 1940. *Arrabidaea verrucosa* (Standl.) A. H. Gentry, Selbyana 2(1): 43, fig. 12d. 1977. *Fridericia verrucosa* (Standl.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Honduras. Atlántida: near Tela, Dec. 1927–Mar. 1928, *P. C. Standley 54891* (holotype, F-584059 image!; isotypes, A not seen, G-8924!, US-1408512 image!).

Nomenclatural note. *Paragonia schumanniana* is the oldest name that applies to this species, but has not been used for it recently because this species has been classified in *Arrabidaea*, where the name *A. schumanniana* Huber was already published for a different species (here called *Bignonia binata* Thunb.) and thus could not be used for this species. The next oldest name for this species is *Adenocalymma verrucosum*, thus in *Arrabidaea* this species was called *Arrabidaea verrucosum*. In *Fridericia* the oldest name can again be used, and the corresponding combination is made here. Type material has not been located for *P. schumanniana*, and further work is needed before the typification of this species can be resolved.

Habitat and distribution. This species is found in humid forest vegetation in Mexico (Chiapas, Oaxaca, Tabasco, Veracruz), Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Chocó, La Guajira, Meta, Nariño), and Venezuela (Apure, Táchira, Zulia), Ecuador, Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno), Bolivia, and Brazil (Acre, Amazonas).

54. Fridericia simplex (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea simplex* A. H. Gentry, Phytologia 46: 206. 1980.

Fridericia simplex (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Goiás [Tocantins]: Parque Nacional do Tocantins, entre a Sede e Veadeiros, 26 Sep. 1967, *J. H. de Haas, Sr., J. H. de Haas & R. B. Belém 344* (holotype, HB not seen; isotype, MO-2698253!).

Habitat and distribution. This species is found in cerrado vegetation in central Brazil (Goiás, Maranhão, Tocantins).

55. Fridericia speciosa Mart., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13: 9, tab. A, 1827. TYPE: Brazil. Rio de Janeiro, *C. F. P. von Martius 358* (*Mart. Herb. Fl. Bras. 448*) (lectotype, designated here, M-86416!; isolectotypes, G-DC!, M-86417!, M-86417 as photo K neg. 4189 at SPF-92651!, MO-1998898!, NY [barcode] NY00328847!, NY [barcode] NY00328848!).

Nomenclatural note. The name *Fridericia guillielma* Mart. was published at the same time as *F. speciosa*; these names were synonymized by Schumann (1894: 222) who chose the name *F. speciosa*. Original material of the type collection is at M. Two duplicates are deposited there, and the best material is here selected as the lectotype.

Habitat and distribution. This species is found in humid to dry forest vegetation in eastern and southeastern Brazil (Bahia, Espírito Santo, Mato Grosso, Minas Gerais, Paraná, Rio de Janeiro, São Paulo).

56. Fridericia spicata (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea spicata* Bureau & K. Schum., Fl. Bras. 8(2): 42. 1896. *Fridericia spicata* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Peru. San Martín: Tarapoto, 1855–1856, *R. Spruce 4535* (holotype, P [barcode] P00468548!; isotypes, BR-876447!, NY [barcode] NY00313120!).

Habitat and distribution. This species is found in wet forest vegetation in Colombia (Amazonas), French Guiana, Ecuador, Peru (Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Amapá, Amazonas, Pará).

57. Fridericia subexserta (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea subexserta* Bureau & K. Schum. Fl. Bras. 8(2): 59. 1896 [1897]. TYPE: Brazil. Near the city of Rio de Janeiro, Mar. 1882, *A. Glaziou 12996* (lectotype, designated here, P [barcode] P00608047!; isolectotypes, F-998521 image!, P [barcode] P00608048!, P [barcode] P00608049!).

Nomenclatural note. Original material of this type collection is at P. Three duplicates are deposited there, and the best material is here selected as the lectotype.

Habitat and distribution. This species is found in dry forest vegetation in Bolivia and southern Brazil (Rio de Janeiro).

58. Fridericia subincana (Mart.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea subincana* Mart., Flora 24(2, Beibl.) 47. 1841. *Fridericia subincana* (Mart.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Rio de Janeiro, 1839, *Herb. Mart. Fl. Bras. 514* (holotype, M-86358!; isotypes, G-DC!, G-DC as photo F neg. 7668 at MO-1692860!, G-9263!, MO-2005569!, NY [barcode] NY00313121!).

Habitat and distribution. This species is found in wet sites in Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Rio de Janeiro, São Paulo).

59. Fridericia subverticillata (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea subverticillata* Bureau & K. Schum., Fl. Bras. 8(2): 24. 1896. *Fridericia subverticillata* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Rio de Janeiro: Teresópolis to São Luiz, Rio Jaú, 18 Jan. 1876, *A. Glaziou 11230* (holotype, P [barcode] P00468549!; isotype, C not seen, C as photo F neg. 22153 at MO-1692861!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Ceará, Piauí, Rio de Janeiro).

60. Fridericia trachyphylla (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Petastoma trachyphyllum* Bureau & K. Schum., Fl. Bras. 8(2): 77. 1896. *Arrabidaea trachyphylla* (Bureau & K. Schum.) Sandwith, Kew Bull. 22: 413. 1968. *Fridericia trachyphylla* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Goiás: Cattus Altas Infiçionado, s.d., *J. E. Pohl 3472* (holotype, W!, W as photo F. neg. 32872 at MO-1693023!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Espírito Santo, Goiás, Minas Gerais, Rio de Janeiro).

61. Fridericia trailii (Sprague) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea trailii* Sprague, Bull. Herb. Boissier, sér. 2, 6: 372. 1906. *Fridericia trailii* (Sprague) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Lower Amazonas, Óbidos, June 1874, *J. W. H. Trail 638* (holotype, K!).

Habitat and distribution. This species is found in humid lowland forest vegetation (Gentry, 1997) in Venezuela (Bolívar), Guyana, Suriname, French Guiana, Peru (Madre de Dios), Bolivia, and Brazil (Acre, Amapá, Amazonas, Pará, Rondônia, Roraima).

62. Fridericia triplinervia (Mart. ex DC.) L. G. Lohmann, comb. nov. Basionym: *Bignonia triplinervia* Mart. ex DC., in A. DC., Prodr. 9: 153. 1845. *Petastoma triplinerve* (Mart. ex DC.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Arrabidaea triplinervia* (Mart. ex DC.) Baill. ex Bureau, Vidensk. Meddel. Dansk Foren. Kjøbenhavn 1893: 99. 1894. *Saritaea triplinervia* (Mart. ex DC.) Dugand, Caldasia 3: 266. 1945. *Fridericia triplinervia* (Mart. ex DC.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia triplinervia* (Mart. ex DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. São Paulo: betw. Paranangaba & Mineiros, Dec. 1817, *C. F. P. von Martius s.n.* (holotype, M-86356!, M-86356 in photo F neg. 20445 at MO-1692863!; isotypes, G-DC!, K!, M-86357!).

Habitat and distribution. This species is found in humid to dry forest vegetation in central Bolivia, Paraguay, Brazil (Amazonas, Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rondônia, São Paulo), and Argentina (Misiones).

63. Fridericia truncata (Sprague) L. G. Lohmann, comb. nov. Basionym: *Mansoa truncata* Sprague, Bull. Herb. Boissier, sér. 2, 5: 83. 1905. *Petastoma truncatum* (Sprague) Hassl., Repert. Spec. Nov. Regni Veg. 9: 53. 1910. *Arrabidaea truncata* (Sprague) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia truncata* (Sprague) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. TYPE: Paraguay. Concepción, Sep. 1901–1902, *E. Hassler 7482* (holotype, K [barcode] K000403426!; isotypes, MO-1573931!, NY [barcode] NY00328881!, NY [barcode] NY00328896!, NY [barcode] NY00328897!, P [barcode] P00481576!, P [barcode] P00481577!).

Habitat and distribution. This species is found in dry forest and Chaco vegetation in Bolivia, Paraguay, and Argentina (Chaco, Jujuy, Salta, Tucumán).

64. Fridericia tuberculata (DC.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea tuberculata* DC., in A. DC., Prodr. 9: 184. 1845. *Fridericia tuberculata* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Pará: s. loc., s.d., *C. F. P. von Martius s.n.* (holotype, G-DC!).

Nomenclatural note. The older name *Bignonia pilulifera* Rich. (Actes Soc. Hist. Nat. Paris 1: 111, 1792) may apply to this species. However, the type of *B. pilulifera* (French Guiana, Cayenne, s.d., *J. B. Le Blond s.n.*, presumably at P) has not yet been located and this situation needs further study.

Habitat and distribution. This species is widely and frequently found in humid forest vegetation in Colombia (Antioquia, Bolívar), Venezuela (Amazonas, Apure, Bolívar), Guyana, Suriname, French Guiana, Ecuador, Peru (Cusco, Huánuco, Loreto, Madre de Dios, Pasco, San Martín), Bolivia, and Brazil (Amapá, Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Rondônia, Roraima).

65. Fridericia tynanthoides (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea tynanthoides* A. H. Gentry, Phytologia 46: 208. 1980. *Fridericia tynanthoides* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 766. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: Pedra Azul, Pedra da Conceição, 20 Apr. 1964, *Z. A. Trinta 762 & E. Fromm 1835* (holotype, HB not seen; isotypes, MO-2692665!, M!, NY [barcode] NY00313124!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Espírito Santo, Minas Gerais).

66. Fridericia viscida (Donn. Sm.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea chica* var. *viscida* Donn. Sm., Bot. Gaz. 20: 7. 1895. *Arrabidaea viscida* (Donn. Sm.) A. H. Gentry, Wrightia 7(2): 84. 1982. TYPE: Guatemala. Santa Rosa: Casillas, 4000 ft., May 1893, *E. T. Heyde 4550* (syntypes, MICH not seen, MO-2005591!, MO- 3168684!, US-1322450 image!, US-1322451 image!).

Nomenclatural note. Two specimens of the type collection from Donnell Smith's herbarium are deposited in US, and further study is needed to clarify the typification of this name.

Habitat and distribution. This species is found in dry forest vegetation in Mexico (Chiapas, Colima, Guerrero, Jalisco, México, Morelos), Belize, Guatemala, Honduras, and Nicaragua.

67. Fridericia whitei (Rusby) L. G. Lohmann, comb. nov. Basionym: *Anemopaegma whitei* Rusby, Mem. New York Bot. Gard. 7: 353. 1927. *Petastoma whitei* (Rusby) Sandwith, Kew Bull. 8(4): 462. 1953 [1954]. *Arrabidaea whitei* (Rusby) Sandwith, Kew Bull. 22: 414. 1968. *Fridericia whitei* (Rusby) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1607. 2008, nom. nud. invalid. TYPE: Bolivia. Beni: Huachi, head of Beni River, 1800 ft., 24 Aug. 1921, *O. E. White 955* (holotype, NY [barcode] NY00313078!; isotype, MICH not seen, MICH as photocopy at MO-2699743!).

Habitat and distribution. This species is found in dry forest vegetation in Bolivia and Paraguay.

IX. Lundia DC., Biblioth. Universelle Genève, sér. 2. 17: 127. 1838, nom. cons., vs. *Lundia* Schumach. (Salicaceae). TYPE: *Lundia glabra* DC., typ. cons. [= *Lundia longa* (Vell.) DC.].

Craterotecoma Mart. ex Meisn., Pl. Vasc. Gen. 1: 300. 1840. TYPE: *Craterotecoma parviflora* DC. [= *Lundia erionema* DC.].

Exsertanthera Pichon, Bull. Soc. Bot. France 92: 226. 1946. TYPE: *Exsertanthera longa* (Vell.) Pichon [≡ *Lundia longa* (Vell.) DC.].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, puberulous to pubescent, densely lenticellate, with interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a simple or trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous or coriaceous, with glands sparsely distributed over lamina, without pellucid punctations, with domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a simple or compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular or tubular, truncate (5-apiculate in *Lundia heliocalyx*) or calyptrate (i.e., splitting transversally) and then becoming truncate through loss of top portion, membranaceous (coriaceous), puberulous to villose externally, without glands; corolla white (magenta, red), with or without nectar guides, tubular or infundibuliform, straight in tube, membranaceous to coriaceous, villose externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included (exserted in *L. longa*), anthers densely villose, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and villose externally, ovules in 2 series on each placenta, stigma rhombic, villose; disk absent. Capsules linear, flattened, straight, coriaceous, with valves 2, puberulous, without lenticels, without glands, without wings, smooth except with midrib developed into a prominent ridge, with calyx caducous; seeds winged, with body smooth and glabrous, wings hyaline, linear.

Number of species, distribution, and habitat. *Lundia* includes 13 species found in wet to dry forest from southern Mexico to southern Brazil.

Lundia is easily recognized by its densely pubescent anthers, ovary, and stigma (synapomorphies of the genus) and its lack of a nectar disk (also a synapomorphy). Additionally the calyx is cupular or tubular in form, with its apex open or calyptrate (i.e., splitting transversally) and eventually having a characteristic essentially truncate form. Also characteristic is the fruit form, with the midrib developed into a prominent ridge; however, this feature can be difficult to observe, because *Lundia* species seem to produce very few fruits under natural conditions (Amaral, 1992; Lopes et al., 2002). Most species of *Lundia* have a bee-pollination floral syndrome (Alcantara & Lohmann, 2010), although a nectar disk is lacking so there may not be a reward for the pollinators; these may be attracted by mimicry and deception (Gentry, 1973a; Vogel, 1993). However *L. longa*, the only hummingbird-pollinated species in the genus, does have a ring of secretory trichomes in the flower that do produce nectar (Lopes et al., 2002). A species-level phylogeny hypothesis of *Lundia* has been published (Kaehler et al., 2012), and a detailed taxonomic revision is expected soon (Kaehler & Lohmann, in prep.). That revision will resolve several long-standing taxonomic problems in *Lundia*, and the species concepts and taxonomy adopted here follow that work. However, the reader should check that revision for updates and details.

1. Lundia corymbifera (Vahl) Sandwith, Receuil Trav. Bot. Néerl. 34: 229. 1937. *Bignonia corymbifera* Vahl, Eclog. Amer. 2: 45, tab. 17. 1798. *Petastoma corymbiferum* (Vahl) Miers,

Proc. Roy. Hort. Soc. London 3: 193. 1863. *Arrabidaea corymbifera* (Vahl) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 213. 1894. *Cuspidaria corymbifera* (Vahl) Baill. ex K. Schum., Nat. Pflanzenfam. 4(3b): 216. 1894. TYPE: Trinidad. s. loc., s.d., *J. P. von Rohr 6* (holotype, C image!, C as photo F neg. 22118 at MO-1692886!).

Bignonia cordata Vell., Fl. Flumin. 247. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 29. 1827 [1831]. *Lundia cordata* (Vell.) DC., in A. DC., Prodr. 9: 180. 1845. TYPE: tab. 29 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Nomenclatural note. The name *Bignonia corymbifera* Vahl is unfortunately the basionym of two combinations published simultaneously in two different genera by Schumann (1894), as clarified by Bureau and Schumann (1896: 37, 157) who noted that the name *Cuspidaria corymbifera* was applied to plants of a different species from *B. corymbifera*. However, their citation and use of the name *C. corymbifera* there satisfy the requirements for valid publication, including being accepted at the time by the authors of the work, in spite of the identity problem they noted and did not resolve. The name *B. cordata* Vell. was applied by Bureau and Schumann (1896) to a different species from *L. corymbifera*, based on a misidentification of Vellozo's original material, but Vellozo's illustration clearly shows the same plants as *L. corymbifera*, and this name is treated as a synonym here. The other species that Bureau and Schumann equated with *B. cordata* is here treated as *L. longa*.

Habitat and distribution. This species is found widely in seasonal forest vegetation (Gentry, 1997) in Costa Rica, Panama, Colombia (Antioquia, Bolívar, César, Chocó, Córdoba, Cundinamarca, Magdalena, Sucre, Tolima, Valle del Cauca), Venezuela (Amazonas, Aragua, Bolívar, Carabobo, Distrito Federal, Falcón, Lara, Miranda, Monagas, Sucre, Trujillo, Yaracuy, Zulia), Trinidad and Tobago, Guyana, French Guiana, Ecuador, Peru (Amazonas, Cajamarca, Cusco, Loreto, Madre de Dios, San Martín, Ucayali), Bolivia, and Brazil (Espírito Santo, Minas Gerais, Rio de Janeiro, Roraima, São Paulo).

2. Lundia damazioi C. DC., Bull. Herb. Boiss., sér 2, 5: 230, fig. 1. 1905, as "*damazii*." TYPE: Brazil. Minas Gerais: Ouro Preto, s.d., *L. B. Damazio 269* (holotype, G not seen, G in photo F neg. 26193 at MO-1692990!; isotypes, F-783905 image!, RB-76446!).

Nomenclatural note. The name *Lundia neolonga* L. G. Lohmann (Cat. Pl. Fung. Brasil 1: 769. 2010, nom. nud. invalid.) has been applied to this species but never formally published and is not needed for it. The original spelling of the species epithet is correctable (McNeill et al., 2006, Art. 60.7).

Habitat and distribution. This species is found in Atlantic forest and cerrado vegetation in southeastern Brazil (Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo).

3. Lundia densiflora DC., in A. DC., Prodr. 9: 181. 1845. TYPE: Brazil. Pará: betw. Sepa & Óbidos, Mar. 1820, *C. F. P. von Martius 3240* (lectotype, designated here, M-86455!, M-86455 in photo F neg. 20469 at MO-169299!; isolectotypes, G-DC!, M-86450!, M-86451!, M-86452!, M-86453!, M-86454!).

Nomenclatural note. Original material of the type collection is at M. Six duplicates are deposited there, and the best material is here selected as the lectotype.

Habitat and distribution. This species is found widely in evergreen lowland to montane forest vegetation (Gentry, 1997) and riparian forests in Colombia (Amazonas, Antioquia, Caquetá, Córdoba, Meta, Santander, Vichada), Venezuela (Amazonas, Bolívar), Guyana, Suriname, Ecuador, Peru (Huánuco, Junín, Loreto, Madre de Dios), Bolivia, and Brazil (Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima).

4. Lundia erionema DC., in A. DC., Prodr. 9: 181. 1845. TYPE: Brazil. Pará: Rio Amazonas, Oct.–Nov., *s. coll. s.n.* (holotype, P!; isotype, G-DC!).

Habitat and distribution. This species is found widely in humid forest vegetation in Colombia (Vaupés), Venezuela (Amazonas, Bolívar), Guyana, Suriname, French Guiana, Ecuador, Peru (Loreto, San Martín), Bolivia, and Brazil (Acre, Pará, Rondônia, Roraima).

5. Lundia gardneri Sandwith, Kew Bull. 9: 601. 1954 [1955]. TYPE: Brazil. Piauí: banks of River Parahim (N of Paranaguá & S of Gurgueia), Sep. 1839, *G. Gardner 2678* (holotype, K!; isotypes, BM!, OXF not seen).

Habitat and distribution. This species is found in cerrado and dry caatinga vegetation in eastern Brazil (Bahia, Minas Gerais, Piauí).

6. Lundia helicocalyx A. H. Gentry, Phytologia 46(4): 210. 1980. TYPE: Brazil. Piauí: Buriti dos Lopes, Canto do Morro, 90–100 m, 20 June 1972, *D. Sucre & J. Silva 9211* (holotype, RB-162875!; isotypes, MO-2630166!, SPF-193218!).

Habitat and distribution. This species is found in cerrado vegetation in northeastern Brazil (Maranhão, Piauí).

7. Lundia laevis Kaehler, Brittonia 63(4): 461, fig. 1. 2011. TYPE: Brazil. Acre: Acrelândia, basin of Rio Madeira, Rio Abunã, Porto Dias, Km. 130 of BR 364, then 30 km on Ramal do Pelé, Colocação Barrinha 3, 9°59′34.4″S, 66°47′53.5″W, 15 May 2009, *D. C. Daly, E. C. Oliveira, A. Sanchez & H. M. Oliveira 13679* (holotype, RB-491535!; isotype, NY not seen).

Taxonomic note. This species was included within the circumscription of *Lundia corymbifera* by Lohmann (2006, 2008b), and sometimes by Gentry in sched. Further field observations will be needed to fully understand the status of these plants.

Habitat and distribution. This species is found in wet, disturbed, lowland vegetation in Brazilian Amazonia (Acre, Pará, Rondônia; Kaehler, 2011).

8. Lundia longa (Vell.) DC., in A. DC., Prodr. 9: 180. 1845. *Bignonia longa* Vell., Fl. Flumin. 249. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 37. 1827 [1831]. *Exsertanthera longa* (Vell.) Pichon, Bull. Soc. Bot. France 92: 226. 1946. TYPE: tab. 37 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Nomenclatural note. The name *Bignonia longa* Vell. was synonymized with the name *Lundia cordata* by Bureau and Schumann (1896: 244), who chose the name *L. cordata*; however, these names actually apply to different species, as discussed in more detail under *L. corymbifera*.

Habitat and distribution. This species is found in wet sites in Atlantic forest vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Paraíba, Pernambuco, Rio de Janeiro, Rio Grande do Norte, São Paulo).

9. Lundia nitidula DC., in A. DC., Prodr. 9: 181. 1845. *Lundia virginalis* var. *nitidula* (DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 64(2): 315. 1977 [1978]. TYPE: Brazil. Sebastianopolis et Minarum General, s.d., *C. F. P. von Martius s.n.* (holotype, M-86444!).

Nomenclatural note. The names *Lundia nitidula* DC. and *L. virginalis* were published simultaneously. These were synonymized by Bureau (1894), who chose *L. nitidula* as the accepted name. Later Gentry (1977) synonymized *L. virginalis* and *L. nitidula* using the name *L. virginalis*, apparently without realizing that Bureau had previously selected the other name. Several morphological differences separate *L. nitidula* and *L. virginalis* (Kaeheler & Lohmann, in prep.) and these are also quite distantly related based on molecular phylogenetic data (Kaeheler et al., 2012).

Habitat and distribution. This species is found in wet sites in Atlantic forest vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Rio de Janeiro, Santa Catarina, São Paulo).

10. Lundia obliqua Sond., Linnaea 22: 561. 1849. TYPE: Brazil. Minas Gerais: near city of Caldas near Capivary, *A. F. Regnell II-192* (lectotype, designated here, BR-876446!).

Nomenclatural note. The specimen *Pohl 6015* has sometimes been regarded in sched. as the type of this name, probably based on Bureau and Schumann's citation of it as the "specimina optima" of this species (1896: 241). However, only one collection was cited by Sonder in the protologue of this name, labeled 195 in Regnell's second series of collections from Brazil. One specimen of this species from Regnell's second series was found at BR and is here designated as the lectotype.

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Minas Gerais, Rio de Janeiro, São Paulo).

11. Lundia puberula Pittier, Contr. U. S. Natl. Herb. 18(6): 258. 1917. TYPE: Panama. Darién: La Palma, southern Darién, 26 Jan. 1912, *H. Pittier 5499* (holotype, US-715745 image!, US-715745 as photo MO neg. 5499 at MO-1183704!; isotypes, F-599461 image!, K!, MO-1167117!).

Habitat and distribution. This species is found widely in humid forest vegetation in Mexico (Quintana Roo, Veracruz), Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Boyacá, Chocó, Magdalena, Meta, Norte de Santander, Santander, Valle del Cauca, Vaupés), Venezuela (Bolívar, Mérida, Miranda, Táchira, Trujillo, Zulia), Ecuador, Peru (Cusco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia).

12. Lundia spruceana Bureau, Adansonia 8: 279. 1868. TYPE: Peru. San Martín: Tarapoto, Jan. 1856, *R. Spruce 4489* (holotype, BR-876413!; isotypes, K [barcode] K000202044!, P [barcode] P00481550!, W not seen, W as photo F neg. 32868 at MO-1692993!).

Habitat and distribution. This species is found in humid forest in Ecuador, Peru (Amazonas, Huánuco, Junín, Loreto, Madre de Dios, San Martín), Bolivia, and western Brazil (Acre).

13. Lundia virginalis DC., Prodr. 9: 181. 1845. *Lundia nitidula* var. *virginalis* (DC.) Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 108. 1894. TYPE: Brazil. Minas Gerais: betw. Tamburil & Valo, s.d., *Wied-Neuwied s.n.* (lectotype, designated here, BR-876246!; isolectotypes, BR-876314!, BR-876347!).

Habitat and distribution. This species is found in cerrado vegetation in eastern Brazil (Bahia, Minas Gerais, Rio de Janeiro).

X. Manaosella J. C. Gomes, Arch. Jard. Bot. Rio de Janeiro 9: 83. 1949. TYPE: *Manaosella platydactyla* (Barb. Rodr.) J. C. Gomes [=*Manaosella cordifolia* (DC.) A. H. Gentry].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, puberulous, without lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds minute or absent, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a multifid tendril, with adhesive disks, without uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary and/or terminal, a raceme. Flowers zygomorphic, pentamerous; calyx spathaceous, membranaceous, puberulent externally, without glands; corolla yellow to magenta, without nectar guides, tubular, straight in tube, membranaceous, glabrous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine psilate; ovary sessile, smooth and lepidote externally, ovules in 2 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, glabrous or puberulous, without lenticels, without glands, without wings, smooth, with calyx persistent; seeds winged, with body smooth and glabrous, wings hyaline, linear. Figure 16E, F.

Number of species, distribution, and habitat. *Manaosella* includes one species found in wet to dry forest vegetation from Venezuela to Bolivia and southeastern Brazil.

Manaosella is monotypic and easily recognized by its multifid tendrils that have adhesive disks on the tips; the combination of these two features is a synapomorphy of the genus. Its yellow flowers, cordate leaflets, racemose inflorescences, relatively large (more than 3 cm long) spathaceous calyx, and linear fruits are each found elsewhere in the tribe, but together aid the identification of *Manaosella*. The phylogenetic hypothesis of the tribe Bignonieae indicates that this is a distinct lineage that has not diversified (Lohmann, 2006).

1. Manaosella cordifolia (DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 65(2): 733. 1978 [1979]. *Bignonia cordifolia* DC., in A. DC., Prodr. 9: 162. 1845. *Stizophyllum cordifolium* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 198. 1863. TYPE: Brazil. Bahia: Serra do Gado Bravo, near Vila Nova da Rainha, Mar., s.d., *C. F. P. von Martius s.n.* (holotype, M-86464!, M-86464 as photo F neg. 20488 at MO-1632885!).

Habitat and distribution. This species is widely found in wet to dry forest vegetation in Venezuela (Amazonas), Bolivia, and Brazil (Amazonas, Bahia, Minas Gerais, Pará, Rio de Janeiro).

XI. Mansoa DC., Biblioth. Universelle Genève, sér. 2, 17: 128. 1838. TYPE: *Mansoa hirsuta* DC. (lectotype, designated by Urban [1916: 745]).

Danielia Corr. Méllo ex Verl., Rev. Hort. 1868: 154. 1868. TYPE: *Danielia splendens* Corr. Méllo ex Verl. [= *Mansoa difficilis* (Cham.) Bureau & K. Schum.].

Hanburyophyton Bureau ex Warm., Vidensk. Medel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 111. 1894. TYPE: *Hanburyophyton xanthinum* Bureau ex Warm., nom. superfl. illeg. [≡ *Mansoa lanceolata* (DC.) A. H. Gentry].

Chodanthus Hassl., Bull. Herb. Boissier, sér. 2, 6: 141. 1906. TYPE: *Chodanthus splendens* (Bureau & K. Schum.) Hassl. [= *Mansoa difficilis* (Cham.) Bureau & K. Schum.].

Pseudocalymma A. Samp. & Kuhlm., Arch. Jard. Bot. Rio de Janeiro 4(11): 15. 1933 [1934], as "*Pseudocalymna*." TYPE: *Pseudocalymma laevigatum* (Bureau & K. Schum.) A. Samp. & Kuhlm. (lectotype, designated by Sampaio & Kuhlmann [1933 (1934): 15]) [= *Mansoa hymenaea* (DC.) A. H. Gentry].

Onohualcoa Lundell, Contr. Univ. Michigan Herb. 7: 52. 1942. TYPE: *Onohualcoa seleri* (Loes.) Lundell [= *Mansoa verrucifera* (Schltdl.) A. H. Gentry].

Bayonia Dugand, Caldasia 4: 62. 1946. TYPE: *Bayonia helicocalyx* (Kuntze) Dugand [= *Mansoa verrucifera* (Schltdl.) A. H. Gentry].

Lianas, without (with, *Mansoa parvifolia*) dimorphic juvenile growth, with garlic odor; stems with phloem wedges in multiples of 4 in cross-section, with solid

pith; branchlets cylindrical with older stems becoming angled and ribbed, glabrous to pubescent, with or without sparsely distributed lenticels, without (with) interpetiolar glands, with (without) discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute or bromeliad-like, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks (with in *M. parvifolia*), without uncinate apices; leaflets chartaceous, with glands grouped in axils of veins, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary, a thyrse (fascicle in *M. parvifolia*). Flowers zygomorphic, pentamerous; calyx cupular, shortly 5-lobed or 5-apiculate, coriaceous or membranaceous, puberulous externally, without glands or with few glands near margins; corolla magenta or pink, without nectar guides, infundibuliform, straight in tube, membranaceous, puberulous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine areolate; ovary sessile, smooth and glabrous externally, ovules in 2 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened or inflated, straight, woody, with valves 2, glabrous or villose, without lenticels, without glands, without wings, smooth except with midrib frequently developed into a prominent ridge, with calyx caducous; seeds winged, with body smooth and glabrous, wings opaque or hyaline, linear. Figure 16A, B.

Number of species, distribution, and habitat. *Mansoa* includes 12 species found in wet to dry forest vegetation from Mexico and the Antilles to Argentina and Brazil.

Mansoa as circumscribed here is characterized by stems that become angular and ribbed with age and have phloem wedges in multiples of 4, branchlets with prominent though discontinuous interpetiolar ridges, prophylls of the axillary buds that are minute and triangular or bromeliad-like, a garlic smell in the foliage (a synapomorphy of the genus), leaflets with subtriplinerved venation and glands in the axils of the basalmost veins, magenta corollas, 2 series of ovules on each placenta, and fruits with the midrib usually developed into a conspicuous ridge.

Gentry (1979, 1997) included *Pachyptera*, *Hanburyophyton*, and *Onhualcoa* within his circumscription of *Mansoa*, based on several morphological characters that overlap between these genera. The phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006) found most of the species traditionally included in *Pachyptera* nested within *Mansoa* except not the type of this genus, *P. kerere* (Aubl.) A. H. Gentry, which was found to be only distantly related to these other species. Consequently, while the circumscription of *Mansoa* adopted here is similar to that of Gentry (1979, 1997), three species are here excluded: *M. erythraea* (Dugand) A. H. Gentry, *M. kerere*, and *M. ventricosa* A. H. Gentry, which are here included in a newly circumscribed *Pachyptera*.

1. **Mansoa alliacea** (Lam.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 782. 1979 [1980]. *Bignonia alliacea* Lam., Encycl. 1: 421. 1785. *Adenocalymma alliaceum* (Lam.) Miers, Ann. Mag. Nat. Hist., ser. 3, 7: 394. 1861. *Pseudocalymma alliaceum* (Lam.) Sandwith, Recueil Trav. Bot. Néerl. 34: 210. 1937. *Pachyptera alliacea* (Lam.) A. H. Gentry, Brittonia 25(2): 236. 1973. TYPE: French Guiana. s. loc., s.d., *J. B. C. F. Aublet s.n.* (holotype, P-LA not seen; isotype, LINN-HS1048-8 fiche!).

Habitat and distribution. This species is found in wet forest vegetation in the Lesser Antilles (Dominica, Martinique, St. Vincent), Costa Rica, Nicaragua, Panama, Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cajamarca, Huánuco, Loreto, Pasco, San Martín), Bolivia, and Brazil (Amazonas, Maranhão, Pará), and is occasionally cultivated.

2. **Mansoa angustidens** (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 200. 1896. *Cuspidaria angustidens* DC., in A. DC., Prodr. 9: 179. 1845. TYPE: Brazil. Pará: Xingú, Aug., *C. F. P. von Martius s.n.* (holotype, M-86461!, M-86461 as photo F 20465 at MO-1692998!).

Habitat and distribution. This species is found in humid forest vegetation in Brazil (Amazonas, Bahia, Ceará, Minas Gerais, Maranhão, Pará, Pernambuco, Piauí, Rio Grande do Norte).

3. **Mansoa difficilis** (Cham.) Bureau & K. Schum., Fl. Bras. 8(2): 201. 1896. *Bignonia difficilis* Cham., Linnaea 7: 714. 1832 [1833]. *Cydista difficilis* (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. TYPE: Brazil. s. loc., 1840, *F. Sellow 6012* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18483 at MO-1692889!, BR-876312!, K!, NY [barcode] NY00483551!).

Habitat and distribution. This species is found frequently in humid forest vegetation in Bolivia, Paraguay, Brazil (Amazonas, Bahia, Ceará, Espírito

Santo, Maranhão, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo), and Argentina (Corrientes, Misiones), and is sometimes cultivated.

4. Mansoa glaziovii Bureau & K. Schum., Fl. Bras. 8(2): 203, tab. 90. 1896. TYPE: Brazil. Minas Gerais: Serra de Ouro Preto, s.d., *A. Glaziou 12991* (lectotype, designated here, P barcode] P00481509!; isolectotypes, F-998955 image!, K!, P [barcode] P00481510!, P as unnumbered sheets in photocopy at MO-2692715!, US-2515579 image!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Glaziou 12991* and *Glaziou 14120*. The more widely distributed collection is here designated as the type, and the best specimen at P is selected as the lectotype.

Habitat and distribution. This species is found in wet forest vegetation in southeastern Brazil (Bahia, Minas Gerais, Rio de Janeiro).

5. Mansoa hirsuta DC., in A. DC., Prodr. 9: 182. 1845. TYPE: Brazil. Bahia: Rio São Francisco, 1838, *J. S. Blanchet 2913* (holotype, G-DC!, G-DC as photo F neg. 7670 at MO-1692996!; isotypes, BM!, K!, P [barcode] P00481513!, P [barcode] P00481514!, P [barcode] P00481515!).

Habitat and distribution. This species is found in dry forest and caatinga vegetation in eastern Brazil (Bahia, Ceará, Mato Grosso, Pernambuco, Piauí).

6. Mansoa hymenaea (DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 782. 1979 [1980]. *Bignonia hymenaea* DC., in A. DC., Prodr. 9: 158. 1945. *Pseudocalymma hymenaeum* (DC.) Sandwith, Candollea 7: 247. 1937. *Pachyptera hymenaea* (DC.) A. H. Gentry, Brittonia 25(3): 236. 1973. *Cuspidaria hymenaea* (DC.) M. R. Almeida, Fl. Maharashtra 3B: 447. 2001. TYPE: Brazil. Bahia: s. loc., 1834, *J. S. Blanchet 1434* (holotype, G-DC!, G-DC as photo F neg. 7635 at MO-1692893!; isotypes, G-8954!, P [barcode] P00481497!, P [barcode] P00481497 as photocopy at MO-2692714!, P [barcode] P00481498!).

Habitat and distribution. This species is found widely in wet to dry forest vegetation in Mexico (Campeche, Chiapas, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Tamaulipas, Veracruz, Yucatán), the Antilles (Grenada, Puerto Rico, St. Lucia), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Venezuela (Distrito Federal, Falcón, Portuguesa), Suriname, French Guiana, Ecuador, Peru (Lambayeque, Madre de Dios, Piura, Puno, Tumbes), and Brazil (Bahia, Espírito Santo, Pará, Rio de Janeiro), and is occasionally cultivated.

7. Mansoa lanceolata (DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 780. 1979. *Tabebuia lanceolata* DC., Biblioth. Universelle Genève, sér. 2, 17: 131. 1838. *Pleonotoma lanceolata* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 184. 1863. *Hanburyophyton xanthinum* Bureau, in Warm., Vidensk. Medel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 111. 1894, nom. superfl. illeg. *Anemopaegma lanceolatum* (DC.) Bureau ex K. Schum., Nat. Pflanzenfam. 4(3b): 215. 1894. TYPE: Brazil. Rio de Janeiro: Santa Tereza, 1834, *P. W. Lund & M. Guillemin 170* (holotype, G-DC!, G-DC as photo F neg. 7689 at MO-1693067!; isotypes, P [barcode] P00481573!, P [barcode] P00481574!, P [barcode] P00481575!).

Habitat and distribution. This species is found in wet sites in Atlantic forest vegetation in eastern Brazil (Bahia, Espírito Santo, Rio de Janeiro).

8. Mansoa montecillensis (Ant. Molina) C. Nelson, Fontqueria 48: 28. 1997. *Chodanthus montecillensis* Ant. Molina, Ceiba 18: 105. 1974. TYPE: Honduras. Comayagua: montaña El Cedral, Cordillera Montecillos, 20 km al S de Siguatepeque, alt. 1500 m, 6 Apr. 1957, *A. Molina R. 8011* (holotype, F not seen; isotype, EAP not seen).

Taxonomic note. This species is recognized here provisionally until its identity can be confirmed.

Habitat and distribution. This species is known from humid forest in Honduras.

9. Mansoa onohualcoides A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 63. 1976. TYPE: Brazil. Ceará: Serra de Baturité, near Sertão do Canindé, 24 Aug. 1908, *A. Ducke s.n.* (holotype, MG-1594!, MG-1594 as photocopy at MO-2436459!; isotype, K!).

Habitat and distribution. This species is found in Atlantic forest vegetation in eastern Brazil (Ceará, Espírito Santo, Maranhão); Gentry (1997) suggested it might also be found in evergreen forest in Venezuela (Amazonas), but this species is circumscribed more narrowly here and that range is excluded.

10. Mansoa parvifolia (A. H. Gentry) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 783. 1979 [1980]. *Pachyptera parvifolia* A. H. Gentry,

Phytologia 26: 447. 1973. TYPE: Colombia. Santander: vic. Puerto Berrio, betw. Rivers Magdalena & Carare, ca. 200 m, 22 Apr. 1937, *O. Haught 2179* (holotype, MO-1188593!; isotype, US-1742407 image!).

Habitat and distribution. This species is found in wet forest vegetation in Guatemala, Honduras, Costa Rica, Panama, Colombia (Antioquia, Chocó, Santander), Ecuador, Peru (Amazonas, Junín, Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Acre, Amazonas).

11. Mansoa standleyi (Steyerm.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 783. 1979. *Pseudocalymma standleyi* Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23(5): 235. 1947. *Pachyptera standleyi* (Steyerm.) A. H. Gentry, Brittonia 25(3): 236. 1973. TYPE: Guatemala. Quetzaltenango: betw. Finca Pirinéos & Finca Soledad, lower S-facing slopes of Volcán Santa María, betw. Santa María de Jesús & Calahuaché, 1300–1400 m, 5 Jan. 1940, *J. A. Steyermark 33533* (holotype, F-1054546 image!; isotypes, F-1054531 image!, F-1054343 image!, US-1894642 image!).

Habitat and distribution. This species is found in forest vegetation (Gentry, 1997) in Guatemala, El Salvador, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Meta, Vichada), Venezuela (Bolívar, Delta Amacuro, Lara, Yaracuy), Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Amazonas, Pará).

12. Mansoa verrucifera (Schltdl.) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 62. 1976. *Bignonia verrucifera* Schltdl., Linnaea 26: 655. 1853. *Adenocalymma verruciferum* (Schltdl.) Miers, Ann. Mag. Nat. Hist., ser. 3, 7: 393. 1861. *Onohualcoa verrucifera* (Schltdl.) A. H. Gentry, Ann. Missouri Bot. Gard. 60(3): 885, fig. 22. 1973 [1974]. TYPE: Venezuela. Aragua: ad Curuciti, ca. 1500 ft., Jan., *H. Wagener 307* (holotype, HAL not seen).

Habitat and distribution. This species is found in semideciduous forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Guerrero, Oaxaca, Quintana Roo, Tabasco, Veracruz, Yucatán), Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Caquetá, César, Chocó, Cundinamarca, Magdalena, Santander, Sucre, Tolima), Venezuela (Amazonas, Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Delta Amacuro, Distrito Federal, Falcón, Guárico, Lara, Miranda, Monagas, Portuguesa, Sucre, Zulia), Trinidad and Tobago, Guyana, Ecuador, Peru (Loreto, Madre de Dios, San Martín), Bolivia, and Brazil (Acre, Amazonas, Mato Grosso, Rondônia), and is sometimes cultivated.

XII. Martinella Baill., Hist. Pl. 10: 30. 1888. TYPE: *Martinella martinii* (DC.) Baill. ex K. Schum. [= *Martinella obovata* (Kunth) Bureau & K. Schum.].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical or tetragonal, glabrous or puberulous, without lenticels, without interpetiolar glands, with a ring-shaped continuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary, a thyrse. Flowers zygomorphic, pentamerous; calyx tubular, irregularly 3- or 4-lobed, membranaceous, puberulent externally, with scattered patelliform glands; corolla magenta, pink, or wine-red, without nectar guides, infundibuliform, straight in tube, membranaceous, glabrous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and lepidote externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, glabrous, without lenticels, with elongated glands, without wings, smooth, with calyx caducous; seeds winged, with body smooth and glabrous, wings opaque, linear.

Number of species, distribution, and habitat. *Martinella* includes two species found in humid forest vegetation from Mexico to Bolivia and Brazil.

Martinella can be readily recognized by the combination of its trifid tendrils, minute triangular prophylls on the axillary buds, a unique interpetiolar ridge that is continuous or ring-shaped and surrounds the stem (a synapomorphy of the genus), and a characteristic bilobed or 3- to 4-parted calyx (a synapomorphy of the genus). Also unusual are the stellate trichomes and the flowers with pink to magenta or wine-colored infundibuliform corollas

that are pollinated by hummingbirds (Gentry, 1990). In the phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006), *Martinella* appears as a distinct lineage that has diversified relatively little.

1. **Martinella iquitoensis** A. Samp., Ann. Acad. Bras. Sci. 7: 122. 1935. *Martinella equitoensis*, orth. var. TYPE: Peru. Loreto: Iquitos, 23 Feb. 1924, *J. G. Kuhlmann 1492* (holotype, RB-22027 [barcode] 5368990!; isotypes, MO-2192060!, RB-22027 [barcode] 537289!).

Habitat and distribution. This species is found in humid vegetation, usually on white sand substrates (Gentry, 1997), in Colombia (Amazonas), Venezuela (Amazonas), Ecuador, Peru (Loreto, Madre de Dios), and Brazil (Amapá, Amazonas, Pará, Rondônia).

2. **Martinella obovata** (Kunth) Bureau & K. Schum., Fl. Bras. 8(2): 161, tab. 84. 1896. *Spathodea obovata* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 147. 1818 [1819]. *Bignonia obovata* (Kunth) Spreng., Syst. Veg. 2: 830. 1825. *Macfadyena obovata* (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 200. 1863. TYPE: Colombia. Magdalena: Turbaco, s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland 1391* (holotype, P-Bonpl.!).

Habitat and distribution. This species is found in humid forest vegetation, sometimes on white sand substrates (Gentry, 1997), in Mexico (Tabasco, Veracruz), Belize, Guatemala, Honduras, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Atlántico, Bolívar, Boyacá, Caquetá, Chocó, Córdoba, Cundinamarca, Guianía, Guaviare, Magdalena, Nariño, Putumayo, Santander, Sucre, Valle del Cauca, Vaupes, Vichada), Venezuela (Amazonas, Anzoátegui, Bolívar, Delta Amacuro, Mérida, Miranda), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia), and is sometimes cultivated.

XIII. Neojobertia Baill., Hist. Pl. 10: 35. 1888. TYPE: *Neojobertia brasiliensis* Baill. [= *Neojobertia candolleana* (Mart. ex DC.) Bureau & K. Schum.]

Gardnerodoxa Sandwith, Kew Bull. 9: 611. 1954 [1955], syn. nov. TYPE: *Gardnerodoxa mirabilis* Sandwith [≡ *Neojobertia mirabilis* (Sandwith) L. G. Lohmann].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets hexagonal, glabrous to glandular-pubescent, without lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds subulate, without glands. Leaves biternately compound or biternately pinnate, terminal division often replaced by a trifid or multifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous or coriaceous, without glands, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, racemose at base and thyrsoid at apex. Flowers zygomorphic, pentamerous; calyx spathaceous and splitting or tubular and shortly 5-lobed, membranaceous, glabrous to pubescent externally, without glands; corolla yellow or red, without nectar guides, tubular or infundibuliform, straight in tube, membranaceous, glabrous or glandular-pubescent externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included or exserted, anthers glabrous, thecae straight, pollen in monads, colpate, with exine areolate; ovary sessile, smooth and glabrous or glandular-pubescent externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, curved, coriaceous, with valves 2, glabrous to glandular-pubescent, without lenticels, without glands, without wings, smooth, with calyx caducous; seeds winged, with body rough and glabrous, wings hyaline or opaque, linear. Figure 16C, D.

Number of species, distribution, and habitat. *Neojobertia* includes two species found in dry forest, caatinga, and savanna vegetation in central to eastern Brazil.

Neojobertia can be recognized by its hexagonal stems with four phloem wedges in cross-section, axillary buds with subulate prophylls, biternately compound or biternately pinnate leaves with a terminal multifid tendril (Fig. 16C), relatively large (more than 3 cm long) spathaceous or tubular calyx (Fig. 16C), yellow or red corollas, uniseriate ovules on the placenta, colpate pollen with areolate or reticulate exine, fruits that are markedly curved and gradually tapered to the apex (a synapomorphy of the genus), unusually long (more than 7 cm) seeds (Fig. 16D), and rough seed surface (Fig. 4B; also a synapomorphy of the genus). The only other members of the tribe Bignonieae with a calyx more than 3 cm long are *Perianthomega*, *Manaosella*, *Callichlamys*, and some species of *Dolichandra*. These other genera can be recognized by the white flowers of *Perianthomega* and the ovule arrangement in the others, biseriate in *Manaosella* and pluriseriate in *Callichlamys* and *Dolichandra* (Table 4).

Sandwith (1954b) in his description of *Gardnerodoxa* considered it different from any other known Bignonieae genus. He did suggest it was related to *Piriadacus erubescens*, which is also hummingbird pollinated and shares the associated floral adaptations with *Gardnerodoxa*; however, these taxa were found to be only distantly related in the phylogenetic hypothesis of Bignonieae (Lohmann, 2006). On the other hand, this phylogenetic hypothesis found *Gardnerodoxa* and *Neojobertia* to be sister taxa, together comprising a single, well-separated clade with a relatively low species diversity. This clade is here recognized as a single genus, based on the taxonomic criteria outlined previously.

1. Neojobertia candolleana (Mart. ex DC.) Bureau & K. Schum., Fl. Bras. 8(2): 396, tab. 109. 1896 [1897]. *Spathodea candolleana* Mart. ex DC., in A. DC., Prodr. 9: 207. 1845. *Memora candolleana* (Mart. ex DC.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. TYPE: Brazil. Piauí: Oeiras, near Terra Nova, Bom Jardim, Mai. 1819, *Herb. Martius Fl. Bras. 2418* (holotype, G-DC!, G-DC as photo F neg. 7692 at MO-1693059!; isotypes, M-86466!, M-86467!, M-86468!, M-86469!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Pernambuco, Piauí).

2. Neojobertia mirabilis (Sandwith) L. G. Lohmann, comb. nov. Basionym: *Gardnerodoxa mirabilis* Sandwith, Kew Bull. 9(4): 611. 1954 [1955]. *Neojobertia mirabilis* (Sandwith) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 770. 2010, nom. nud. invalid. TYPE: Brazil. Piauí: near Alagadões, ca. 100 mi. SW of Oeiras, July 1839, *G. Gardner 2677* (holotype, K!; isotypes, BM!, P [barcode] P00481462!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Espírito Santo, Maranhão, Piauí).

XIV. Pachyptera DC. ex Meisn., Pl. Vasc. Gen 1: 299. 1840. TYPE: *Pachyptera foveolata* DC. (lectotype, designated by Sandwith [1932: 84]) [= *Pachyptera kerere* (Aubl.) Sandwith].

Sererea Raf., Sylva Tellur. 107. 1838. TYPE: *Sererea heterophylla* Raf., nom. illeg. superfl. [≡ *Pachyptera kerere* (Aubl.) Sandwith].

Leucocalantha Barb. Rodr., Vellosia, ed. 2. 1: 46. 1891, syn. nov. *Leucocalanthe*, orth. var. TYPE: *Leucocalantha aromatica* Barb. Rodr. [≡ *Pachyptera aromatica* (Barb. Rodr.) L. G. Lohmann].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical or tetragonal, glabrous, without lenticels, with interpetiolar glands, with or without discontinuous interpetiolar ridge, with epidermis or bark peeling when older; prophylls of axillary buds triangular and minute or ensiform and rigid, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous or coriaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a raceme. Flowers zygomorphic, pentamerous; calyx tubular, minutely 5-lobed, coriaceous, puberulent externally, with patelliform glands arranged in lines near margins; corolla white, without nectar guides, narrowly tubular, straight in tube, membranaceous, puberulous to villose externally, with glands arranged in lines on upper portion of tube, lobes 5, imbricate; stamens 4, with well-developed filaments, exserted, anthers puberulous or glabrous, thecae straight, pollen in monads, colpate, with exine psilate; ovary sessile, smooth and lepidote externally, ovules in 1 series on each placenta, stigma lanceolate, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, woody, with valves 2, glabrous, without lenticels, with scattered glands, without ridges, without wings, smooth, with calyx caducous; seeds winged and linear or wingless and round, with body smooth and glabrous, wings when present opaque. Figure 17A, B.

Number of species, distribution, and habitat. *Pachyptera* includes four species found in wet and flooded forest vegetation from Central America to Bolivia and Brazil.

Pachyptera can be recognized by stems with four phloem wedges in cross-section, bark that is papery and peels as the branchlets age, interpetiolar glands, trifid tendrils, prophylls of the axillary buds that are flattened and ensiform (Fig. 17B) or minute and triangular, white tubular corollas (Fig. 17A, B) with glands arranged in lines in the upper portion of the corolla tube, tubular truncate calyces with conspicuous glands arranged in lines on the upper portion, and linear fruits with glands scattered throughout the surface. The flowers in this genus are apparently all moth pollinated, which suggests that flower form and pollination mode may sometimes be consistent within a clade in Bignonieae.

Pachyptera has not been recognized as a separate genus by recent authors. In particular, Gentry (1979)

included all of *Pachyptera* within his circumscription of *Mansoa* based on several morphological characters that overlap between these genera. Here *Pachyptera* is separated again but circumscribed differently from any previous taxonomy, based on the phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006). The genus here includes three species that have been classified in *Pachyptera*, plus one species that was previously separated as *Leucocalantha*. The other species that have been included at various times in *Pachyptera* are here classified in *Mansoa*, as discussed under that genus.

These relationships found by the phylogenetic hypothesis (Lohmann, 2006) were initially surprising, although Santos (1995) noted that the wood anatomy of the plants she studied as *Mansoa kerere* (i.e., *Pachyptera kerere*) is quite different from that of the other *Mansoa* species she analyzed. This wood differed in its four phloem wedges versus multiples of four in the other species of *Mansoa*, its vessels with a long radial alignment, and the silica bodies in its wood. In general presumed relationships based on single morphological characters in this tribe should be taken with caution, but the number of phloem wedges appears to be quite stable phylogenetically in Bignonieae (Pace et al., 2009, 2011) so the inclusion of this species in *Mansoa* was highly suspect all along. *Leucocalantha aromatica* also has four phloem wedges along with the other characteristic features of *P. kerere*. The wood of the other species that have been included in *Mansoa* was also surveyed, and two additional species not previously studied, *M. erythraea* and *M. ventricosa*, were found to have the characters of *Pachyptera*, and are also included in this genus here.

1. **Pachyptera aromatica** (Barb. Rodr.) L. G. Lohmann, comb. nov. Basionym: *Leucocalantha aromatica* Barb. Rodr., Vellosia (ed. 2) 1: 47, t. 7. 1891. *Pachyptera aromatica* (Barb. Rodr.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 770. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: close to Manaus, July, *J. Barbosa Rodrigues 633* (holotype, not located).

Habitat and distribution. This species is found in wet forest vegetation in Amazonian Brazil (Amazonas, Rondônia).

2. **Pachyptera erythraea** (Dugand) A. H. Gentry, Phytologia 35(3): 186, fig. 2A. 1977. *Pachyptera kerere* var. *erythraea* Dugand, Caldasia 7(31): 16. 1955. *Mansoa erythraea* (Dugand) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 782. 1979 [1980]. TYPE: Colombia. Santander: SE of Barranca Bermeja, 9 km from lt. bank of River Opón, 200 m, 26 Aug. 1954, *R. Romero-Castañeda 4727* (holotype, COL-47378 image!).

Habitat and distribution. This species is found in wet forest vegetation in northern Colombia (Antioquia, Santander).

3. **Pachyptera kerere** (Aubl.) Sandwith, Recueil Trav. Bot. Néerl. 34: 219. 1937. *Bignonia kerere* Aubl., Hist. Pl. Guiane 2: 644, tab. 260. 1775, as "*cherere*" in plate. *Bignonia heterophylla* Willd., Sp. Pl. 3: 298. 1800 [1801], nom. superfl. illeg. *Sererea heterophylla* Raf., Sylva Tellur. 107. 1838, nom. superfl. illeg. *Adenocalymma kerere* (Aubl.) Bureau & K. Schum., Fl. Bras. 8(2): 119. 1891. *Petastoma kerere* (Aubl.) Schnee, in H. Pittier et al., Cat. Fl. Venez. 2: 404. 1947. *Mansoa kerere* (Aubl.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 783. 1979 [1980]. TYPE: French Guiana. s. loc., s.d., *J. B. C. F. Aublet s.n.* (holotype, BM!; isotype, LINN-1048/5 fiche!).

Habitat and distribution. This species is found in humid and often flooded forest vegetation (Gentry, 1997) in Belize, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Caquetá, Casanare, Chocó, Guianía, Nariño, Vaupes, Vichada), Venezuela (Amazonas, Anzoátegui, Apure, Bolívar, Delta Amacuro, Mérida, Táchira), Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, Ucayali), Bolivia, and Brazil (Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima).

4. **Pachyptera ventricosa** (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Mansoa ventricosa* A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 783. 1979 [1980]. TYPE: Brazil. Pará: along Belém–Brasilia hwy., Km. 345, 9 Aug. 1963, *B. Maguire, J. Murça Pires, C. K. Maguire & N. T. Silva 56083* (holotype, MO-2232816!; isotypes, NY-328882!, US-3189002 image!).

Habitat and distribution. This species is known only from wet forest vegetation in a small area of northeastern Brazil (Pará).

XV. Perianthomega Bureau ex Baill., Hist. Pl. 10: 33. 1888. TYPE: *Perianthomega vellozoi* (Vell.) Bureau (lectotype, designated by Bureau [1894: 105]).

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem arcs in cross-

section, pith solid; branchlets cylindrical, glabrous or lepidote, covered with lenticels, without interpetiolar glands, without interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves biternately compound, without tendrils; leaflets chartaceous, without glands, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, frequently becoming twining and woody, not articulated. Inflorescence terminal, a raceme. Flowers zygomorphic, pentamerous; calyx tubular, shortly 5-lobed, membranaceous, puberulent externally, without glands; corolla white, without nectar guides, tubular, straight in tube, membranaceous, glabrous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and puberulous externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, glabrous, with lenticels, without glands, without ridges, without wings, smooth, with calyx caducous; seeds winged, with body smooth and glabrous, wings hyaline, linear. Figure 17C–E.

Number of species, distribution, and habitat. *Perianthomega* includes one species found in dry vegetation from Bolivia to southeastern Brazil.

Perianthomega is distinguished by its leaves that are always biternately compound, twining petioles modified into a simple tendril (a synapomorphy of the genus), a large (more than 3 cm) tubular calyx, and large white corollas (more than 6 cm long) (Fig. 17C). The only other genera that have species with equally large tubular calyces are *Neojobertia*, *Manaosella*, *Dolichandra*, and *Callichlamys*; however, the species with a similar calyx in those genera all differ in their yellow or red flowers.

Baillon (1888), Schumann (1894), and Bureau and Schumann (1896) included *Perianthomega* in the tribe Bignonieae, but Gentry (1980) considered *Perianthomega* to be intermediate between the tribes Bignonieae and Tecomeae in its wood anatomy and fruit morphology. He later transferred this genus to the tribe Tecomeae, because he thought the wood anatomy lacked the phloem wedges of Bignonieae and the fruit dehiscence seemed to be loculicidal (Gentry, 1992c). However, molecular phylogenetic analyses of the tribe Bignonieae (Lohmann, 2006) as well as the whole Bignoniaceae (Olmstead et al., 2009) found that *Perianthomega* is sister to the core members of Bignonieae (i.e., the tribe as previously circumscribed) and best placed in this tribe. These results are supported by morphology because *Perianthomega* does have the two characters that diagnose this tribe, the septicidal fruits (Fig. 17E) and discontinuous phloem arcs (Fig. 17D).

1. Perianthomega vellozoi Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 105. 1893 [1894], replacement name. *Bignonia perianthomega* Vell., Fl. Flumin. 248. 1825 [1829], Fl. Flumin. Icon. 6: tab. 34, 1827 [1831]. *Memora perianthomega* (Vell.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. TYPE: tab. 34 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Nomenclatural note. Botanical names may not be tautonyms (McNeill et al., 2006, Art. 23.4), so Bureau had to create a new species epithet when he classified *Bignonia perianthomega* in a genus with the same name as its species epithet. Gentry in sched. annotated the collection *Glaziou 11246* as the type of *Perianthomega vellozoi*, based on a citation of this collection by Bureau (1894). However, Bureau's name *P. vellozoi* was based on *B. perianthomega* Vell., and therefore must be typified by Vellozo's materials. In this particular work Bureau cited a voucher specimen, usually a Glaziou collection, for each species he listed, but he did not present any discussion or indication that he intended to designate any types for these names. Vellozo's name is here lectotypified by his original material, which has priority over a new collection (McNeill et al., 2006, Art. 9.10).

Habitat and distribution. This species is found in dry vegetation in the Andean foothills of southern Bolivia and in northern Paraguay and Brazil (Espírito Santo, Mato Grosso, Mato Grosso do Sul, Minas Gerais).

XVI. Pleonotoma Miers, Proc. Roy. Hort. Soc. London. 3: 184. 1863. TYPE: *Pleonotoma jasminifolia* (Kunth) Miers (lectotype, designated by Sandwith [1962: 457]).

Nestoria Urb., Ber. Deutsch. Bot. Ges. 34: 751. 1916. TYPE: *Nestoria obtusifoliolata* (Bureau & K. Schum.) Urb. [= *Pleonotoma albiflora* (Salzm. ex DC.) A. H. Gentry].

Kuhlmannia J. C. Gomes, Notul. Syst. (Paris) 15: 222. 1956. TYPE: *Kuhlmannia colatinensis* J. C. Gomes [= *Pleonotoma albiflora* (Salzm. ex DC.) A. H. Gentry].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets tetragonal with angles acute and winged, glabrous (puberulous to pubescent), without lenticels, without interpetiolar glands,

with discontinuous interpetiolar ridge, with epidermis or bark peeling at least on stem angles; prophylls of axillary buds foliaceous, with glands. Leaves biternately compound or biternately pinnate, terminal division often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous, with glands distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole tetragonal, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, an elongated (congested) raceme. Flowers zygomorphic, pentamerous; calyx cupular or tubular, shortly 5-lobed, membranaceous, glabrous to villose externally, with glands in lines near margins; corolla white, cream, or yellow, without nectar guides, tubular, straight in tube, membranaceous, glabrous to puberulous externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and lepidote externally, ovules in 2 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, woody, with valves 2, glabrous, without lenticels, without glands, without wings, smooth, with calyx caducous; seeds winged, with body smooth and glabrous, wings opaque, linear.

Number of species, distribution, and habitat. *Pleonotoma* includes 17 species found in wet to dry forest, caatinga, and cerrado vegetation from northern Central America to southern Brazil.

Pleonotoma is strongly supported as monophyletic in the phylogenetic hypothesis of Bignonieae (Lohmann, 2006) and readily identifiable based on vegetative characters. It is the only genus in the tribe with the combination of markedly tetragonal stems with the corners winged (a synapomorphy of the genus) and the epidermis or bark peeling especially along these corners, tetragonal petioles (another synapomorphy), and biternately compound or biternately pinnate leaves. The showy white to yellow, tubular flowers of *Pleonotoma* are likely pollinated by bees and hawkmoths (Gentry, 1974a). The fruits of *Pleonotoma* are linear and the seeds are unusually large, more than 10 cm long. Only *Neojobertia* has equally long seeds; it can be separated by its hexagonal stems.

Pleonotoma has sometimes been included within *Memora* (which is here included within *Adenocalymma*) based on its biternately compound or biternately pinnate leaves and racemose inflorescences. However, the phylogenetic hypothesis of Bignonieae (Lohmann, 2006) found that these genera are not closely related, and their separation is also supported by morphological characters: *Pleonotoma* lacks the volcano-shaped glands that are a synapomorphy of *Adenocalymma* (Fig. 3A); also *Pleonotoma* has ovules that are biseriate on the placentas and colpate pollen, in contrast to the uniseriate ovules and inaperturate pollen of *Adenocalymma*.

1. Pleonotoma albiflora (Salzm. ex DC.) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 71. 1976. *Bignonia albiflora* Salzm. ex DC., in A. DC., Prodr. 9: 167. 1845. *Memora albiflora* (Salzm. ex DC.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. *Nestoria albiflora* (Salzm. ex DC.) Sandwith, Candollea 7: 248. 1936. TYPE: Brazil. Bahia: s. loc., 1830, *P. Salzmann 346* (holotype, G-DC!, G-DC as photo F neg. 7674 at MO-1692877!; isotypes, P [barcode] P00410842!, P [barcode] P00410841!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) and Atlantic forest vegetation in Venezuela (Amazonas, Bolívar, Delta Amacuro), Guyana, Suriname, French Guiana, and Brazil (Amazonas, Bahia, Espírito Santo, Pará).

2. Pleonotoma bracteata A. H. Gentry, Phytologia 46(4): 213. 1980. TYPE: Brazil. Amazonas: Óbidos, Serra da Escama, 9 Sep. 1928, *A. J. Sampaio 4909* (holotype, R not seen; isotype, MO-2305576!).

Habitat and distribution. This species is found in wet forest vegetation in northeastern Brazil (Amazonas, Pará).

3. Pleonotoma castelnaei (Bureau) Sandwith, Kew Bull. 13: 438. 1958 [1959]. *Pleonotoma variabilis* var. *castelnaei* Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 105. 1893 [1894]. TYPE: Brazil. s. loc., s.d., *A. Glaziou 9952* (holotype, P [barcode] P00410840!, P as photo K neg. 3127 at K!; isotype, C!).

Habitat and distribution. This species is found in dry caatinga and cerrado vegetation in eastern Brazil (Bahia, Maranhão, Minas Gerais, Piauí).

4. Pleonotoma clematis (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 184. 1863. *Bignonia clematis* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 141. 1818 [1819]. TYPE: Venezuela. Guárico: Llanos de Calabozo, betw. Calabozo & River Guárico, Apr., *F. W. H. A. von Humboldt & A. J. A. Bonpland 777* (holotype, P-Bonpl.!, P-Bonpl.

as photo F neg. 39409 at MO-1692932!; isotype, B-W-11473!).

Habitat and distribution. This species is found in semideciduous to deciduous forest vegetation (Gentry, 1997) in Colombia (Norte de Santander, Vaupés), Venezuela (Amazonas, Anzoátegui, Apure, Bolívar, Guárico, Miranda, Monagas, Sucre), Guyana, Suriname, French Guiana, and Brazil (Amapá, Amazonas, Rondônia, Roraima).

5. Pleonotoma dendrotricha Sandwith, Mem. New York Bot. Gard. 10(1): 141. 1958. TYPE: Venezuela. Amazonas: Río Orinoco, 1–10 km below San Fernando de Atabapo, 150 m, 11 May 1954, *J. Silverio Level 67* (holotype, K!; isotype, NY [barcode] NY00328900!).

Habitat and distribution. This species is found in humid forest vegetation, often on white sand substrates (Gentry, 1997), in Colombia (Guainía, Vaupés), Venezuela (Amazonas), French Guiana, Peru (Loreto, Puno, Ucayali), Bolivia, and Brazil (Amazonas, Pará, Rondônia).

6. Pleonotoma echitidea Sprague & Sandwith, Bull. Misc. Inform. Kew 1934: 102. 1934. TYPE: British Guiana [Guyana]. Upper Demerara River, Sep. 1887, *G. S. Jenman 4124* (holotype, K!).

Habitat and distribution. This species is found in wet forest vegetation in Guyana and Suriname.

7. Pleonotoma exserta A. H. Gentry, Mem. New York Bot. Gard. 29(1): 281, fig. 124D. 1978. TYPE: Venezuela. Amazonas: rd. from San Fernando de Atabapo to Santa Barbara, 12–40 km from San Fernando, 110 m, 24 Mar. 1974, *A. H. Gentry & S. S. Tillett 10865* (holotype, MO-2241755!; isotypes, MO-2241753!, MO-2241754!, MBM not seen, NY [barcode] NY01085444!, VEN not seen, XAL not seen).

Habitat and distribution. This species is found in savanna vegetation on white sand substrates in Colombia (Caquetá, Guainía), Venezuela (Amazonas, Bolívar), and Brazil (Amazonas).

8. Pleonotoma fissicalyx B. M. Gomes & Proença, Kew Bull. 65(2): 272, fig. 1. 2010. TYPE: Brazil. Pará: ca. 18 km E of Tucuruí & Tocantins River, by BR-263, 3°30′S, 49°32′W, 28 Oct. 1981, *D. C. Daly, R. Callejas, M. G. da Silva, E. L. Taylor, C. Rosario & D. M. R. dos Santos 991* (holotype, MG not seen; isotypes, MO-3002537!, NY not seen).

Taxonomic note. This material was first identified as a new species of *Pleonotoma* by A. H. Gentry, who annotated specimens in sched. with the unpublished epithet "macrosiphon."

Habitat and distribution. This species is found in humid vegetation on white sand substrates in northeastern Brazil (Pará).

9. Pleonotoma fluminensis (Vell.) A. H. Gentry, Taxon 24(4): 342. 1975. *Bignonia fluminensis* Vell., Fl. Flumin. 246. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 39. 1827 [1831]. *Memora fluminensis* (Vell.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863. TYPE: tab. 39 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Minas Gerais, São Paulo).

10. Pleonotoma jasminifolia (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 184. 1863, *jasminifolium*, orth. var. *Bignonia jasminifolia* Kunth, Nov. Gen. Sp. Pl. (quarto ed.) 3: 141. 1818 [1819]. TYPE: Venezuela. Amazonas: San Fernando, betw. rivers Orinoco & Atabapo, May 1800, *F. W. H. A. von Humboldt & A. J. A. Bonpland 1010* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39413 at MO-1692926!; isotype, B-W-11471!).

Habitat and distribution. This species is found in wet forest vegetation, usually on sandy substrates (Gentry, 1997), in Colombia (Amazonas, Caquetá, Cundinamarca, Meta, Vaupés, Vichada), Venezuela (Amazonas, Bolívar), and Brazil (Amazonas, Pará, Rondônia).

11. Pleonotoma longiflora B. M. Gomes & Proença, Kew Bull. 65(2): 273, fig. 2. 2010. TYPE: Brazil. Amazonas: rd. Manaus–Itacoatiara, Km. 26, Ducke forest reserve, 2°53′S, 59°58′W, 9 July 1997, *R. C. Forzza 290* (holotype, UB not seen; isotypes, INPA-191275 not seen, MO-6223722!, NY not seen).

Habitat and distribution. This species is found in wet lowland forest vegetation in the central Amazon basin of Brazil (Amazonas).

12. Pleonotoma melioides (S. Moore) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 42. 1976. *Bignonia melioides* S. Moore, Trans. Linn. Soc. London, Bot., Ser. 2, 4: 414. 1895. TYPE: Brazil. Mato Grosso: near Santa Cruz, Oct.

1891–1892, *S. Moore 406* (holotype, BM [barcode] 000882583 image!).

Habitat and distribution. This species is found in wet forest vegetation and Atlantic forest vegetation in Colombia (Amazonas, Caquetá), Ecuador, Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Bahia, Espírito Santo, Goiás, Maranhão, Mato Grosso, Pará, Rondônia).

13. Pleonotoma orientalis Sandwith, Brittonia 3(2): 92. 1938. TYPE: Brazil. Maranhão: Ilha do Trauira, Maracassumé River, 30 Aug. 1932, *R. Froes 1840* (holotype, NY [barcode] NY00328903!; isotypes, BM!, F-707102 image!, K!, MO-1041515!, P [barcode] P00481544!, US-1663967 image!).

Habitat and distribution. This species is found on rocky outcrops in central Brazil (Bahia, Goiás, Maranhão, Pará).

14. Pleonotoma pavettiflora Sandwith, Bull. Misc. Inform. Kew 1934: 103. 1934. TYPE: Brazil. Mato Grosso: NE of Cuiabá, Burity, 2250 ft., June 1927, *G. D. Smith 294* (holotype, K!).

Habitat and distribution. This species is found in humid forest vegetation in Bolivia and Brazil (Acre, Mato Grosso, Rondônia).

15. Pleonotoma stichadenia K. Schum., Nat. Pflanzenfam. 4(3b): 226. 1894, as "*stichadenium*." TYPE: Brazil: Espírito Santo, betw. Campos & Vitória, s.d., *F. Sellow 417* (holotype, B†, B as photo F neg. 18436 at MO-1693040!; lectotype, designated here, K [barcode] K000449777!).

Nomenclatural note. The presumed holotype specimen documented in the collection at B by a photograph has been destroyed. No duplicates were found at P, where Schumann's collaborator Bureau worked; consequently, the duplicate at K is here chosen as the lectotype.

Habitat and distribution. This species is found in humid vegetation and Atlantic forest vegetation in Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Pará, Pernambuco, Rio de Janeiro).

16. Pleonotoma tetraquetra (Cham.) Bureau, J. Soc. Imp. Centr. Hort., Ser. II, 2: 156. 1868. *Bignonia tetraquetra* Cham., Linnaea 7: 675. 1832 [1833]. *Memora tetraquetra* (Cham.) Miers, Proc. Hort. Soc. London 3: 185. 1863. TYPE: Brazil. Minas Gerais: Lagoa Santa, 1840, *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, B as photo F neg. 18437 at MO-1693041!, K!, NY [barcode] NY00328752!).

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Minas Gerais, Rio de Janeiro, São Paulo).

17. Pleonotoma variabilis (Jacq.) Miers, Proc. Hort. Soc. London 3: 184. 1863. *Bignonia variabilis* Jacq., Pl. Hort. Schoenb. 2: 45, tab. 212. 1797. TYPE: Venezuela. Caracas, s.d., *N. J. Jacquin s.n.* (holotype, W!).

Habitat and distribution. This species is found in evergreen lowland forest vegetation (Gentry, 1997) in Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Caldas, Caquetá, Chocó, Córdoba, Cundinamarca, La Guajira, Magdalena, Santander, Tolima), Venezuela (Amazonas, Apure, Aragua, Bolívar, Carabobo, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Táchira, Trujillo, Yaracuy, Zulia), Trinidad and Tobago, Ecuador, Peru (Loreto, Madre de Dios, Pasco, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Pará).

XVII. Pyrostegia C. Presl, Abh. Köenigl. Böhm. Ges. Wiss., ser. 5, 3: 523. 1845. TYPE: *Pyrostegia ignea* (Vell.) C. Presl [= *Pyrostegia venusta* (Ker Gawl) Miers].

Lianas, without dimorphic juvenile growth, without strong odor; stems with phloem wedges in multiples of 4 in cross-section, pith solid; branchlets hexagonal, glabrous to puberulous, without lenticels, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds triangular and minute, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina or grouped in axils of veins, with pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a corymbiform cyme. Flowers zygomorphic, pentamerous; calyx cupular, shortly 5-lobed, membranaceous, puberulent externally, without glands; corolla orange-red or white, without nectar guides, narrowly tubular, straight in tube, membranaceous, glabrous externally except puberulous on margins of lobes, without glands, lobes 5, valvate at base and imbricate above; stamens 4, with well-developed filaments, exserted, anthers glabrous,

thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and lepidote externally, ovules in 1 series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous, with valves 2, glabrous, with lenticels, without glands, without wings, smooth, with calyx persistent; seeds winged, with body smooth and glabrous, wings hyaline, linear.

Number of species, distribution, and habitat. *Pyrostegia* includes two species found in dry to humid vegetation from Mexico to Argentina.

Pyrostegia can be recognized by its minute triangular prophylls of the axillary buds, hexagonal stems, 2- or 3-foliolate and pellucid-punctate leaves with the terminal leaflet often replaced by a trifid tendril, inflorescences arranged in corymbose cymes (a synapomorphy of the genus), and unusual corolla lobe arrangement. The corolla lobes are valvate in bud at their bases, but then shift to imbricate at their apices (Pool, 2008). This arrangement is a synapomorphy of the genus and a unique feature in this tribe. The flowers are variously orange and hummingbird pollinated, or white and moth pollinated (Gentry, 1990).

The genus *Pyrostegia* is circumscribed here similarly to Pool (2008), except *P. cinerea* is classified in *Cuspidaria* based on the phylogenetic hypothesis of the tribe Bignonieae (Lohmann, 2006). Pellucid-punctate leaves are also found in *Stizophyllum*, but *Stizophyllum* can be recognized by its distinctive hollow stems, versus solid stems in *Pyrostegia*.

1. Pyrostegia millingtonioides Sandwith, Kew Bull. 15: 464. 1962. TYPE: Brazil. Pará: Óbidos, 23 July 1912, *A. Ducke s.n. MG-12046* (holotype, K!; isotype, MG-12046 not seen).

Habitat and distribution. This species is found apparently infrequently in disturbed and successional areas in humid vegetation in northeastern Brazil (Maranhão, Pará).

2. Pyrostegia venusta (Ker Gawl.) Miers, Proc. Roy. Hort. Soc. London 3: 188. 1863. *Bignonia venusta* Ker Gawl., Bot. Reg. 3, tab. 249. 1817 [1818]. *Tecoma venusta* (Ker Gawl.) Lem., Hort. Universel 5: 1. 1843. TYPE: tab. 249 in Ker Gawler, Bot. Reg. 3, 1818, "drawn from cultivated specimens growing at British Gardens," i.e., cultivated at Coombe Wood, England, from seeds collected in Rio de Janeiro, Brazil (lectotype, designated by Sandwith & Hunt [1974: 75]).

Pyrostegia dichotoma Miers ex K. Schum., Nat. Pflanzenfam. 4(3b): 223. 1894, syn. nov. TYPE: Peru. San Martín: Tarapoto, 1855–1856, *R. Spruce 3930* (lectotype, designated by Pool [2008: 502], G not seen, G as photo F neg. 26203 not seen; isolectotypes, BM not seen, BR not seen, G-DC not seen, K not seen, NY-278040!, P not seen, W not seen).

Tynanthus igneus Barb. Rodr., Vellosia, ed. 2, 1: 50, 3: ser. 2: tab. 10. 1891, non *Pyrostegia ignea* (Vell.) C. Presl, 1845. TYPE: Brazil. Amazonas: ad ripas Rio Negro prope Manaus, *J. Barbosa Rodrigues s.n.* (holotype, INPA not seen).

Nomenclatural note. Pool (2008: 498, 501) noted that the Amazonian specimens of Barbosa Rodrigues have been sought for many years and are all considered to be lost, and accordingly she designated a lectotype for *Tynanthus igneus* and selected the illustration in the protologue of this name. However, Pool (pers. comm.) subsequently discovered that a single Barbosa Rodrigues collection did survive at INPA, as detailed by Mori and Ferreira (1987), and this specimen coincidentally is the type of *T. igneus*. Mori and Ferreira confirmed that all the Amazonian specimens stored in the INPA herbarium were lost, but Barbosa Rodrigues's library there survived and this one specimen was for some reason left in the library.

Taxonomic note. *Pyrostegia dichotoma* and *P. venusta* were separated by Pool (2008) based on the level of staminode insertion and details of the stem trichomes. However, field observations on the flowers (L. G. Lohmann, pers. obs.) found extensive variation in the level of staminode insertion within local populations of these plants in various parts of Brazilian Amazonia, and found no correlation between this and any other features or habitat preferences. The pubescence details cited by Pool do not alone support the separation of two species here, and these names are thus considered synonyms. Further study with additional sources of data will be necessary to understand this species complex.

Habitat and distribution. This species is widely and commonly found in dry to humid lowland forests in Mexico (Chiapas, México, Michoacán, Morelos, Oaxaca, Sinaloa, Veracruz), Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia (Caquetá, Meta, Valle del Cauca), Venezuela (Amazonas, Bolívar, Delta Amacuro, Distrito Federal, Miranda, Sucre, Táchira), Guyana, Suriname, Ecuador, Peru (Cusco, Huánuco, La Libertad, Lambayeque, Lima, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, Paraguay, Brazil (Acre, Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Rondônia,

Roraima, Santa Catarina, São Paulo, Tocantins), and Argentina (Corrientes, Jujuy, Misiones, Tucumán), and is widely cultivated elsewhere.

XVIII. Stizophyllum Miers, Proc. Roy. Hort. Soc. London. 3: 197. 1863. TYPE: *Stizophyllum perforatum* (Cham.) Miers (lectotype, designated by Baillon [1888: 30]).

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, with hollow pith; branchlets cylindrical, pubescent, without lenticels, without interpetiolar glands, without interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds foliaceous, without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina, with pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary and/or terminal, a lax to congested, few-flowered raceme. Flowers zygomorphic, pentamerous; calyx urceolate, irregularly bilabiate to 5-lobed, membranaceous, puberulent or villose externally, without glands; corolla white, pink, or magenta, without nectar guides, infundibuliform, straight in tube, membranaceous, pubescent externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine reticulate; ovary sessile, smooth and lepidote externally, ovules in 2 series on each placenta, stigmas elliptic, glabrous; disk annular. Capsules linear, narrow, flattened, straight, coriaceous, with valves 2, puberulous to villose, without lenticels, without glands, without wings, smooth, with calyx persistent; seeds winged, with body smooth and glabrous, wings hyaline, linear.

Number of species, distribution, and habitat. *Stizophyllum* includes three species found in wet to dry forest and disturbed vegetation from Mexico to southern Brazil. Species of *Stizophyllum* usually are pioneers, occupying large patches in disturbed areas, borders of forests, and other secondary vegetation.

The circumscription of *Stizophyllum* has not been controversial. The genus is easily recognizable by its hollow stems and branchlets (both synapomorphies of the genus), pellucid-punctate leaflets, and trifid tendrils. The racemose inflorescences, urceolate calyx, usually pink to magenta corolla, and linear fruits are also useful in its identification.

1. Stizophyllum inaequilaterum Bureau & K. Schum., Fl. Bras. 8(2): 221. 1896. TYPE: Peru. Loreto: Maynas, 1831, *E. F. Poeppig 1827* (holotype, W!, W as photo F neg. 32877 at MO-1693064!; isotypes, F-875529 image!, IT not seen).

Habitat and distribution. This species is found in humid lowland to premontane forest vegetation (Gentry, 1997) and is particularly abundant in disturbed and second-growth vegetation, in Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Chocó, Meta, Valle del Cauca), Venezuela (Amazonas, Bolívar), Suriname, French Guiana, Ecuador, Peru (Amazonas, Huánuco, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amapá, Amazonas, Pará, Rondônia, Roraima).

2. Stizophyllum perforatum (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 198. 1863. *Bignonia perforata* Cham., Linnaea 7: 667. 1832 [1833]. TYPE: Brazil. s. loc., 1840, *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, K!, NY [barcode] NY00313145!).

Nomenclatural note. The names *Bignonia perforata* and *B. physaloides* Cham. were published simultaneously; these were synonymized by Bureau and Schumann (1896: 220), who chose *B. perforata*.

Habitat and distribution. This species is found widely but apparently sporadically in humid forest and disturbed vegetation in Mexico (Campeche), Guatemala, Costa Rica, Panama, Guyana, Brazil (Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Paraná, Piauí, Rio de Janeiro, São Paulo).

3. Stizophyllum riparium (Kunth) Sandwith, Lilloa 3: 462. 1938. *Bignonia riparia* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 138. 1818 [1819]. TYPE: Colombia. Bolívar: Río Magdalena, near Mompox, May 1801, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P-Bonpl.!, P-Bonpl. as photo F neg. 39424 at MO-1692925!).

Habitat and distribution. This species is found in humid forest and disturbed vegetation in Mexico (Campeche, Chiapas, Oaxaca, Quintana Roo, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Bolívar, Boyacá, Caquetá, Chocó, Cundinamarca, Santander, Sucre, Tolima), Venezuela (Amazonas, Barinas, Bolívar, Táchira), Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amapá, Ama-

zonas, Bahia, Espírito Santo, Maranhão, Mato Grosso, Pará, Rio de Janeiro, São Paulo).

XIX. Tanaecium Sw., Prodr. Veg. Ind. Occ. 6: 91. 1788, emend. L. G. Lohmann. TYPE: *Tanaecium jaroba* Sw.

Paragonia Bureau, Bull. Soc. Bot. France 19: 17. 1872, syn. nov. TYPE: *Bignonia lenta* Mart. ex DC. [= *Tanaecium pyramidatum* (Rich.) L. G. Lohmann].

Sanhilaria Baill., Hist. Pl. 10: 27. 1888. *Hilariophyton* Pichon, Bull. Soc. Bot. France 92: 228. 1946, nom. illeg. superfl. TYPE: *Sanhilaria brasiliensis* Baill. [≡ *Tanaecium brasiliensis* (Baill.) L. G. Lohmann].

Ceratophytum Pittier, J. Wash. Acad. Sci. 18: 62. 1928, syn. nov. TYPE: *Ceratophytum capricorne* Pittier [= *Tanaecium tetragonolobum* (Jacq.) L. G. Lohmann].

Periarrabidaea A. Samp., Ann. Acad. Brasil. Sci. 6: 175. 1934, syn. nov. TYPE: *Periarrabidaea truncata* A. Samp. (lectotype, designated here) [≡ *Tanaecium truncatum* (A. Samp.) L. G. Lohmann].

Spathicalyx J. C. Gomes, Notul. Syst. (Paris) 15: 220. 1956, syn. nov. TYPE: *Spathicalyx kuhlmannii* J. C. Gomes [= *Tanaecium duckei* (A. Samp.) L. G. Lohmann].

Pseudocatalpa A. H. Gentry, Brittonia 25(3): 241. 1973, syn. nov. TYPE: *Pseudocatalpa caudiculata* (Standl.) A. H. Gentry [≡ *Tanaecium caudiculatum* (Standl.) L. G. Lohmann].

Lianas, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical (tetragonal in *Tanaecium caudiculatum*), glabrous or pubescent, with sparsely distributed lenticels, with or without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds subulate and/or bromeliad-like, with or without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a simple, minutely bifid, or trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous to subcoriaceous, with glands sparsely distributed over lamina (grouped in axils of veins in *T. xanthophyllum*), without pellucid punctations, with or without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a thyrse or cyme. Flowers zygomorphic, pentamerous; calyx cupular, bilabiate, coriaceous, puberulous or villose externally, with fields of glands or without glands; corolla yellow, white, pink, or magenta, without nectar guides, tubular or infundibuliform, straight in tube, membranaceous, villose externally, without glands, lobes 5, imbricate; stamens 4 (2 in *T. caudiculatum*), with well-developed filaments, included (exserted in *T. caudiculatum*), anthers glabrous, thecae straight, pollen in monads, colpate, with exine psilate or reticulate; ovary sessile, smooth and lepidote externally, ovules in 1(2) series on each placenta, stigma ellipsoid, glabrous; disk annular. Capsules linear (elliptic in *T. caudiculatum*), flattened or inflated, straight, woody or coriaceous, with valves 2, puberulous, with lenticels, without glands, without wings, smooth, with calyx caducous; seeds winged or wingless, with body smooth and glabrous, wings hyaline or opaque, linear, wingless seeds corky and rounded. Figure 18A–C.

Nomenclatural notes. Baillon (1888) cited *Bignonia lenta* as the type of *Paragonia* but did not explicitly associate the name of the genus with the epithet of this species as required for valid publication of a combination (McNeill et al., 2006, Art. 33.1). The name *B. lenta* has since been considered a synonym of *P. pyramidata* (Rich.) Bureau, and consequently the name *B. lenta* was never transferred to *Paragonia*; however, this does not preclude its being the type of *Paragonia*.

Pichon (1946) considered the name *Sanhilaria* Baill. to be a later homonym of *Sanhilaria* Leandro ex DC., a name supposedly published in 1838 for a genus of Asteraceae, and he therefore published the replacement name *Hilariophyton* for the genus of Bignoniaceae. This conclusion was based on his survey of annotations of herbarium specimens deposited at P. However, the supposedly earlier name was never validly published. It was mentioned in one published work, where it was cited as an unpublished name that had been informally used for plants of *Stifftia* J. K. Mikan (Asteraceae), but this mention does not constitute valid publication.

The genus *Periarrabidaea* was described with two species, and apparently no lectotype has been designated until now.

Number of species, distribution, and habitat. *Tanaecium* includes 17 species found in wet to dry forest vegetation from Mexico and the Antilles to Argentina.

Tanaecium is well characterized by the prophylls of the axillary buds that are usually mixed subulate and bromeliad-like (a synapomorphy of the genus; Fig. 18B), wood with four phloem wedges in cross-section, well-developed interpetiolar ridges, leaflets with straight-percurrent venation and sparsely distributed glands, thick bilabiate calyx, villose corolla, colpate pollen, pubescent fruits, and opaque corky seeds. Well-developed interpetiolar glands and terminal inflorescences are also generally present.

Tanaecium is here circumscribed more broadly than previously, to include the species usually classified here along with four species that were previously placed in *Arrabidaea* and also the formerly recognized genera *Ceratophytum*, *Pseudocatalpa*, *Spathicalyx*, *Paragonia*, and *Periarrabidaea*. Gentry (1973a) previously suggested that *Tanaecium*, *Para-*

gonia, and *Ceratophytum* were closely related based on their trifid tendrils, white flowers, wood with four phloem wedges, and similar growth form as what he termed giant bush ropes. The close relationship of these and *Pseudocatalpa*, *Periarrabidaea*, *Spathicalyx*, and the several species previously placed in *Arrabidaea* was not suspected before, but is well supported by molecular phylogenetic data (Lohmann, 2006) and the morphological characters listed above. *Pseudocatalpa caudiculata* Standl. was always considered unusual in Bignonieae in its flowers with only two stamens, but it has the diagnostic morphological features of *Tanaecium*.

1. Tanaecium affine (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea affinis* A. H. Gentry, Novon 2(2): 159. 1992. TYPE: Ecuador. Sucumbíos: banks of Lake Agrio, 250 m, 0°07′N 76°55′W, 1 Apr. 1980, *J. Brandbyge & E. Asanza 30393* (holotype, MO-3096367!; isotypes, AAU not seen, AAU as photocopy at MO-3003444!, NY-106!).

Habitat and distribution. This species is found in forest vegetation in Colombia (Amazonas, Meta), Ecuador, Peru (Amazonas, Junín, Loreto, Madre de Dios, Pasco, Puno), and Bolivia.

2. Tanaecium apiculatum A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 58, fig. 4. 1976. TYPE: Venezuela. Monagas: Caicara, 15 May 1952, *F. D. Smith 226* (holotype, US-2121468 not seen, US-2121468 as photocopy at MO-2228969!; isotype, US-2121469 image!, US-2121469 as photocopy at MO-2228970!).

Habitat and distribution. This species is found in wet forest vegetation in eastern Venezuela (Monagas).

3. Tanaecium bilabiatum (Sprague) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008. *Memora bilabiata* Sprague, Bull. Herb. Boissier, sér. 2, 6: 375. 1906. *Adenocalymma bilabiatum* (Sprague) Sandwith, Recueil Trav. Bot. Néerl. 34: 213. 1937. *Arrabidaea bilabiata* (Sprague) Sandwith, Kew Bull. 22: 418. 1968. TYPE: Brazil. Amazonas: Manaus, s.d., *R. Spruce 1783* (holotype, K not seen).

Habitat and distribution. This species is found in wet and flooded lowland forest vegetation (Gentry, 1997) in Colombia (Amazonas, Arauca, Guainía), Venezuela (Amazonas, Apure, Bolívar, Delta Amacuro, Guárico, Monagas, Sucre), Guyana, Suriname, French Guiana, Peru (Loreto, Madre de Dios), Bolivia, and Brazil (Acre, Amapá, Amazonas, Pará, Roraima).

4. Tanaecium caudiculatum (Standl.) L. G. Lohmann, comb. nov. Basionym: *Petastoma caudiculatum* Standl., Field Mus. Nat. Hist., Bot Ser. 11(4): 141. 1932. *Mussatia caudiculata* (Standl.) Seibert, Publ. Carnegie Inst. Wash. 522: 418. 1940. *Pseudocatalpa caudiculata* (Standl.) A. H. Gentry, Brittonia 25(3): 241. 1973. TYPE: Belize. Nine Mile, Stann Creek Railway, 30 m, 22 Mar. 1932, *W. A. Schipp S-297* (holotype, F-657811 image!; isotype, F-657912 image!).

Habitat and distribution. This species is found in wet forest vegetation in Mexico (Oaxaca, Veracruz), Belize, and Guatemala.

5. Tanaecium crucigerum Seem., Bonplandia (Hannover) 4: 127. 1856. TYPE: Lesser Antilles. Dominica, s. loc., s.d., *J. Imray 95* (lectotype, selected by Howard [1989: 334], K not seen).

Nomenclatural note. Some confusion surrounds the nomenclatural history and typification of this name. *Bignonia crucigera* L. was described in the first edition of the *Species Plantarum* (Linnaeus, 1753), and was lectotypified following its circumscription in this work by Barrie et al. (1991) so its identity is clear. In a later edition of the *Species Plantarum*, Linnaeus (1763: 869) treated this same species but with a different circumscription, and cited the same references to its identity as previously, plus a new one, Plumier's Icones 48, tab. 58. *Bignonia crucigera* was later studied by de Candolle (1845: 152), who revised its circumscription significantly: he excluded all of the original elements (i.e., the names and figures that detailed the species) that were cited by Linnaeus, and he applied this name only to the species in Plumier's plate. Thus, de Candolle's use of the name *B. crucigera* was a misidentification, because the plants he included under this name must match at least one of Linnaeus's type elements from the original (1753) circumscription of this species in order for this name to correctly applied, but de Candolle specifically excluded those. The plants that de Candolle included in his new circumscription of the species he incorrectly called *B. crucigera* were later described and detailed by Seemann (1852–1857), who called them *Tanaecium crucigerum*. Because de Candolle misidentified these plants, the name *B. crucigera* does not apply to them so they did not have a validly published name until Seemann named them. Seemann's name was thus not based on Linnaeus's name *B. crucigera*, and is nomenclaturally separate from that. Seemann cited three elements to identify his species *T. crucigera*: Plumier's plate, some unspecified materials from Dominica collected by Imray, and some unspecified

materials from St. Vincent collected by Guilding. Seemann's collections are mainly deposited at BM, but are found widely elsewhere as well (Stafleu & Cowan, 1985: 474). The Guilding collections have not been found. Two collections of Dr. John Imray's from Dominica that were part of Hooker's herbarium are imaged on the web at K, *Imray 94* and *Imray 4* (both databased there as Imary). These are both annotated with the name *T. crucigerum* and a reference to Plumier's plate. Howard (1989: 334) lectotypified Seemann's name on the specimen *Imray 95*, but this particular collection has not been located in this study. Further work will be needed to either locate this lectotype specimen at K, or confirm that Howard incorrectly cited the type number.

Habitat and distribution. This species is found in humid forest vegetation in the Lesser Antilles (Dominica, Martinique), Colombia (Atlántico, Bolívar, César, Magdalena), Venezuela (Anzoátegui, Apure, Cojedes, Delta Amacuro, Guárico, Portuguesa), and Trinidad and Tobago.

6. Tanaecium cyrtanthum (Mart. ex DC.) Bureau & K. Schum, Fl. Bras. 8(2): 186. 1896. *Tecoma cyrtantha* Mart. ex DC., in A. DC., Prodr. 9: 218. 1845. TYPE: Brazil. Bahia: Pão d'Espinho, Oct., *C. F. P. von Martius 1860* (holotype, M-88980!, M-88980 as photo F neg. 20463 at MO-1693071; isotype, G-DC!).

Habitat and distribution. This species is found in dry forest and caatinga vegetation in Bolivia, Paraguay, Brazil (Bahia, Ceará, Pernambuco, Rio Grande do Norte), and Argentina (Salta).

7. Tanaecium duckei A. Samp., Ann. Acad. Brasil. Sci. 7: 125. 1935. *Spathicalyx duckei* (A. Samp.) A. H. Gentry, Phytologia 35(3): 194. 1977. TYPE: Brazil. Pará: Óbidos, 21 July 1918, *A. Ducke s.n.* (holotype, MG-17137; isotypes, K!, MO-2192052!, RB-22695).

Habitat and distribution. This species is found in wet forest vegetation in Colombia (Amazonas), Peru (Loreto, Pasco), and Brazil (Amazonas, Minas Gerais, Pará, Rio de Janeiro).

8. Tanaecium exitiosum Dugand, Caldasia 1(5): 31, fig. 1. 1942. TYPE: Colombia. Santander: Barrancabermeja, 50 m, 5 Apr. 1942, *R. Mora s.n.* (holotype, COL-10017 image!).

Habitat and distribution. This species is found in humid forest vegetation in northern Colombia (Antioquia, Caldas, Santander).

9. Tanaecium jaroba Sw., Prodr. 92: 1788, as "Iaroba." TYPE: Jamaica. s. loc., s.d., *O. Swartz s.n.* (holotype, S not seen).

Habitat and distribution. This species is found in swampy and flooded forest vegetation (Gentry, 1997) in the Antilles (Jamaica, St. Vincent), Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Atlántico, Bolívar, Caquetá, La Guajira, Magdalena, Sucre), Venezuela (Amazonas, Apure, Bolívar, Carabobo, Delta Amacuro, Guárico, Zulia), Trinidad and Tobago, Guyana, French Guiana, Ecuador, Peru (Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Amazonas, Mato Grosso, Pará, Roraima).

10. Tanaecium mutabile (Bureau & K. Schum.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea mutabilis* Bureau & K. Schum., Fl. Bras. 8(2): 38. 1896. *Fridericia mutabilis* (Bureau & K. Schum.) L. G. Lohmann, Monogr. Syst. Bot. Missouri Bot. Gard. 107(2): 1606. 2008, nom. nud. invalid. *Fridericia mutabilis* (Bureau & K. Schum.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 765. 2010, nom. nud. invalid. TYPE: Brazil. São Paulo: Campinas, s.d., *J. Correia de Méllo 44* (lectotype, designated here, P [barcode] P00468542!; isolectotypes, P [barcode] P00468543!, P [barcode] P00468544!, P [barcode] P00468545!, P [barcode] P00468546!, S not seen, S as photocopy at MO-2909990!).

Nomenclatural note. Two syntypes were cited in the protologue of this name, *Correia de Mello 44* and *Balansa 405*, from Paraguari near Yanguaron in Paraguay (G-DC not seen, G-DC as photo F neg. 26170 at MO-1692794!, K not seen, K as photocopy at MO-2904352!). The collection found at P is here designated as the type because it is more likely to be part of Bureau's original material of this species. Five duplicates are deposited at P, and the only flowering material is here selected as the lectotype. This species was sometimes provisionally included in *Fridericia* by Lohmann (Arbo & Lohmann, 2008; Lohmann, 2010; in sched.), but recent detailed study confirms its classification in *Tanaecium*.

Habitat and distribution. This species is found occasionally in seasonal vegetation in Bolivia, Paraguay, Brazil (Acre, Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo), and Argentina (Corrientes, Misiones, Salta).

11. Tanaecium neobrasiliense L. G. Lohmann, nom. nov. Replaced name: *Sanhilaria brasiliensis* Baill., Hist. Pl. 10: 27. 1888, non *Tanaecium brasiliense* Miers, 1891. *Hilariophyton brasilien-*

sis (Baill.) Pichon, Bull. Soc. Bot. France 92: 228. 1946, nom. superfl. illeg. *Paragonia brasiliensis* (Baill.) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 70. 1976. *Tanaecium neobrasiliense* L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 771. 2010, nom. nud. invalid. TYPE: Brazil. Minas Gerais: s. loc., 1816–1821, *A. St. Hilaire 745* (holotype, P [barcode] P00468597!; isotype, P [barcode] P00468598!).

Habitat and distribution. This species is found in cerrado vegetation in eastern Brazil (Bahia, Ceará, Minas Gerais).

12. Tanaecium pyramidatum (Rich.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008. *Bignonia pyramidata* Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792. *Tabebuia pyramidata* (Rich.) DC., in A. DC., Prodr. 9: 214. 1845. *Paragonia pyramidata* (Rich.) Bureau, Konigl. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd., ser. 6, 6: 422. 1892. TYPE: French Guiana. Cayenne, s.d., *J. B. Leblond 292* (holotype, P-LA!).

Habitat and distribution. This species is found in dry to evergreen lowland to montane forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Colima, Oaxaca, Quintana Roo, Tabasco, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Amazonas, Antioquia, Atlántico, Boyacá, Caquetá, Chocó, Córdoba, Cundinamarca, Guaviare, Magdalena, Meta, Nariño, Putumayo, Santander, Valle del Cauca, Vaupés), Venezuela (Amazonas, Anzoátegui, Apure, Barinas, Bolívar, Delta Amacuro, Distrito Federal, Falcón, Lara, Miranda, Monagas, Portuguesa, Sucre, Yaracuy, Zulia), Trinidad and Tobago, Guyana, Suriname, French Guiana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, Paraguay, Brazil (Acre, Amapá, Amazonas, Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo), and Uruguay. This is one of the most widespread and commonly collected species in this tribe.

13. Tanaecium revillae (A. H. Gentry) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea revillae* A. H. Gentry, Ann. Missouri Bot. Gard. 65(2): 726, fig. 1. 1978 [1979]. *Tanaecium revillae* (A. H. Gentry) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 771. 2010, nom. nud. invalid. TYPE: Peru. Loreto: Maynas, distr. Pebas, Río Yahuasyacu, afluente del Río Ampiyacu, 18 July 1976, *J. Revilla 718* (holotype, MO-2416649!; isotypes, COL not seen, F-1797223 image!, NY [barcode] NY00313111!, UNAP not seen, USM not seen).

Habitat and distribution. This species is found in wet and flooded lowland forest vegetation in Guyana, Suriname, Peru (Loreto), and Brazil (Amazonas, Pará).

14. Tanaecium selloi (Spreng.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008. *Bignonia selloi* Spreng., Syst. Veg. 2: 831. 1825. *Arrabidaea selloi* (Spreng.) Sandwith, Kew Bull. 8(4): 461. 1953 [1954]. TYPE: Brazil. s. loc., 1840, *F. Sellow s.n.* (holotype, B†; lectotype, designated here, L-898196-295 image!; isolectotype, L-898196-296 image!).

Nomenclatural note. The holotype of *Bignonia selloi* was destroyed at B, but duplicates were located at L and the best flowering material is here designated as the lectotype.

Habitat and distribution. This species is found in semideciduous and dry forest vegetation in Colombia (Bolívar), Venezuela (Falcón, Lara, Zulia), Peru (Cusco), Bolivia, Paraguay, Brazil (Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Mato Grosso do Sul, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo), and Argentina (Chaco, Corrientes, Jujuy, Misiones, Salta).

15. Tanaecium tetragonolobum (Jacq.) L. G. Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008. *Bignonia tetragonoloba* Jacq., Fragm. Bot. 36, tab. 40, fig. 2. 1809 [1810]. *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandwith, Bull. Misc. Inform. Kew 1934: 222. 1934. TYPE: tab. 40, fig. 2 in N. J. Jacquin, Fragm. Bot. 36, 1809 [1810] (lectotype, designated here).

Habitat and distribution. This species is found in dry to evergreen lowland forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Quintana Roo, Tabasco, Yucatán), the Antilles (Grenada), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Atlántico, Bolívar, Chocó, La Guajira, Magdalena, Meta, Santander, Sucre), Venezuela (Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Portuguesa, Táchira, Yaracuy, Zulia), Trinidad and Tobago, Guyana,

Suriname, Ecuador, Peru (Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, and Brazil (Pará, Rondônia).

16. **Tanaecium truncatum** (A. Samp.) L. G. Lohmann, comb. nov. Basionym: *Periarrabidaea truncata* A. Samp., Bol. Mus. Nac. Rio de Janeiro 12: 86. 1936. *Tanaecium truncatum* (A. Samp.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 771. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Manaus, Villa Municipal, 27 July 1931, *A. Ducke s.n. in RB-24093* (holotype, R-24093!).

Habitat and distribution. This species is found in humid forest vegetation in Ecuador, Peru (Cusco, Huánuco, Loreto, Madre de Dios, Ucayali), Bolivia, and Brazil (Amazonas, Goiás, Maranhão, Mato Grosso, Pará, Rondônia).

17. **Tanaecium xanthophyllum** (DC.) L. G. Lohmann, comb. nov. Basionym: *Tabebuia xanthophylla* DC., in A. DC., Prodr. 9: 214. 1845. *Arrabidaea xanthophylla* (DC.) Bureau & K. Schum., Fl. Bras. 8(2): 70. 1896. *Xylophragma xanthophylla* (DC.) J. F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13 (pt. 5c, no. 1): 65. 1961, as "*xanthophyllum*." *Spathicalyx xanthophylla* (DC.) A. H. Gentry, Phytologia 35(3): 195. 1977. *Tanaecium xanthophyllum* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 771. 2010, nom. nud. invalid. TYPE: Brazil. Amazonas: Alto Amazonas, Rio Negro, Maribi, towards River Japurá, Dec. 1819, *C. F. P. von Martius 2967* (holotype, G-DC!, G-DC as photo F neg. 7686 at MO-1692866!; isotypes, M-88929!, M-88930!, M-88931!, M-88932!, M-88933!, M-88934!, M-88935!).

Habitat and distribution. This species is found in wet forest vegetation in Colombia (Amazonas, Putumayo), Ecuador, Peru (Amazonas, Cusco, Junín, Loreto, Madre de Dios, San Martín, Ucayali), Bolivia, and Brazil (Amazonas, Maranhão).

XX. Tynanthus Miers, Proc. Roy. Hort. Soc. London. 3: 193. 1863, *Tynnanthus*, orth. var. TYPE: *Tynanthus fasciculatus* (Vell.) Miers (lectotype, designated by Sandwith [1962: 454]).

Schizopsis Bureau, Monogr. Bignon. 44. 1864. TYPE: *Schizopsis labiata* (Cham.) Bureau ex Baill. [≡ *Tynanthus labiatus* (Cham.) Miers].

Lianas, without dimorphic juvenile growth, with strong clove odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical (to angled and flattened in *Tynanthus polyanthus*), pubescent, sparsely to densely lenticellate, without interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds foliaceous or minute and triangular, with or without glands. Leaves 2- or 3-foliolate, terminal leaflet often replaced by a trifid tendril, tendrils without adhesive disks, without uncinate apices; leaflets chartaceous, with glands sparsely distributed over lamina, without pellucid punctations, without domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence axillary or terminal, a compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular, truncate (5-denticulate in *T. fasciculatus*), membranaceous, puberulent to villose externally, without glands; corolla white, without nectar guides, infundibuliform, bilabiate, and short (less than 1 cm), curved in tube, membranaceous, villose externally, without glands, lobes 5 with upper 2 fused, imbricate; stamens 4, with well-developed filaments, exserted, anthers glabrous, thecae forward-curved, pollen in monads, colpate, with exine psilate; ovary sessile, smooth and villose externally, ovules in 2 series on each placenta, stigma rhombic, glabrous; disk poorly developed. Capsules linear, flattened, straight, coriaceous, with valves 2, puberulous to villose, without lenticels, without glands, with margins raised to developed into wings, smooth, with calyx caducous; seeds winged, with body smooth and glabrous, wings hyaline, linear. Figure 18D, E.

Number of species, distribution, and habitat. *Tynanthus* includes 15 species found in wet to dry forest vegetation from southern Mexico to Bolivia and southern Brazil.

Tynanthus is characterized by its strong smell of cloves (a synapomorphy of the genus), generally cylindrical branchlets (later becoming angled to flattened in *T. polyanthus*), trifid tendrils, relatively small (less than 1 cm long) bilabiate corollas with the two upper lobes fused (also a synapomorphy; Fig. 18E), a poorly developed nectar disk, and fruits with characteristic raised margins that are frequently developed into conspicuous wings (also a synapomorphy). Winged fruits are otherwise found only in *Cuspidaria* and *Fridericia*, but in those genera the wings develop from the midrib rather than the margins and the tendrils are simple. *Tynanthus* is well circumscribed, but its species limits are not clear, at least in part because most of the species are not well known.

The spelling of *Tynanthus* has sometimes been confused. At the time of its publication it was written as Tynanthus, which is the accepted spelling.

However, subsequent authors have frequently misspelled the name as Tynnanthus.

1. Tynanthus cognatus (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 193. 1863. *Bignonia cognata* Cham., Linnaea 7: 703. 1832 [1833]. TYPE: Brazil. s. loc., s.d., *F. Sellow 166* (holotype, LE not seen; isotypes, B†, G as photo F neg. 18479 at MO-1692884!, K!, K as photocopy at MO-2904325!).

Habitat and distribution. This species is found in humid forest vegetation in southeastern Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo).

2. Tynanthus croatianus A. H. Gentry, Ann. Missouri Bot. Gard. 58(1): 93, fig. 1. 1971. TYPE: Panama. Canal Zone [Panamá]: shoreline NE of Drayton House on Barro Colorado Island, 28 Aug. 1970, *T. B. Croat 11927* (holotype, MO-2039180!; isotypes, F-1697804 image!, K!, MO-2016962!, MO-2042197!, MO-2042198!, NY-328978!, US-2620246 image!).

Habitat and distribution. This species is found in lowland humid forest vegetation in Costa Rica, Panama, and Colombia (Chocó).

3. Tynanthus elegans Miers, Proc. Roy. Hort. Soc. London 3: 193. 1863. *Bignonia elegans* Cham., Linnaea 7: 702. 1832 [1833], nom. illeg., non *Bignonia elegans* Vell., 1825 [1829]. TYPE: Brazil. s. loc., s.d., *F. Sellow 5596* (holotype, LE not seen; isotype, B†, B as photo F neg. 18585 at MO-1692891!).

Nomenclatural note. The collection number of the type was not specified in the protologue, but the specimen at B that was numbered 5596 was considered a duplicate of the type by A. H. Gentry in sched. and his annotation is provisionally followed here. An ongoing taxonomic revision of the genus will further clarify its typification (Medeiros & Lohmann, in prep.).

Habitat and distribution. This species is found in humid forest vegetation in southeastern Brazil (Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Santa Catarina, São Paulo).

4. Tynanthus fasciculatus (Vell.) Miers, Proc. Roy. Hort. Soc. London 3: 193. 1863. *Bignonia fasciculata* Vell., Fl. Flumin. 247. 1825 [1829]; Fl. Flumin. Icon. 6: tab. 25. 1827 [1831]. *Arrabidaea fasciculata* (Vell.) DC., in A. DC., Prodr. 9: 185. 1845. *Cuspidaria fasciculata* (Vell.) Sond., Linnaea 22: 560. 1849. TYPE: tab. 25 in Vellozo, Fl. Flumin. Icon. 6, 1827 [1831] (lectotype, designated here).

Habitat and distribution. This species is found in humid forest vegetation in southeastern Brazil (Minas Gerais, São Paulo).

5. Tynanthus goudotianus (Bureau) Bureau, Adansonia 8: 274. 1868, as "*goudotiana*." *Tynanthus gondotiana*, orth. var. *Schizopsis goudotiana* Bureau, Adansonia 5: 374. 1865. *Schizopsis gondotiana*, orth. var. TYPE: Nouvelle-Granade [Colombia]. s. loc., May–June 1844, *J. Goudot s.n.* (holotype, P!, P as photocopy at MO-2909992!, P as photo F neg. 39957 at K!).

Habitat and distribution. This species is found in humid forest vegetation in Colombia (Amazonas, Caquetá) and Brazil (Amazonas).

6. Tynanthus guatemalensis Donn. Sm., Bot. Gaz. 18(1): 6. 1893. TYPE: Guatemala. Quezaltenango: Río Ocosito, 250 ft., Apr. 1892, *J. Donnell Smith 1488* (holotype, US-1322405 image!; isotypes, GH not seen, M!, NY [barcode] NY00328979!, P [barcode] P00468599!, US-48056 image!).

Habitat and distribution. This species is found in humid forest vegetation in Mexico (Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz), in Belize and Guatemala.

7. Tynanthus labiatus (Cham.) Miers, Proc. Roy. Hort. Soc. London 3: 193. 1863. *Bignonia labiata* Cham., Linnaea 7: 701. 1832 [1833]. *Schizopsis labiata* (Cham.) Bureau ex Baill., Adansonia 5: 373. 1864 [1865]. TYPE: Brazil. s. loc., s.d., *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, G-DC!, K!, K as photocopy at MO-2904326!, NY [barcode] NY00579087!).

Habitat and distribution. This species is found in Atlantic forest vegetation in southeastern Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, Santa Catarina, São Paulo).

8. Tynanthus macranthus L. O. Williams, Fieldiana, Bot. 31(10): 250. 1967. TYPE: Costa Rica. Heredia: 8 km S of San Miguel, 800 m, 9 July 1964, *R. W. Lent 42* (holotype, F-1622130 image!; isotypes, NY [barcode] NY00328981! OKL not seen, US-2964011 image!).

Habitat and distribution. This species is found in cloud forest vegetation in the Cordillera de Talamanca of Costa Rica and western Panama.

9. Tynanthus micranthus Corr. Méllo ex K. Schum, Nat. Pflanzenfam. 4(3b): 221. 1894, as "micrantha." TYPE: Brazil. São Paulo: Campinas, 9 Mar. 1867, *J. Correia de Méllo 26* (lectotype, designated here, P [barcode] P00481491!; isolectotypes, K [barcode] K000449546!, P [barcode] P00481488!, P [barcode] P00481489!, P [barcode] P00481490!, P [barcode] P00481481 not seen, P [barcode] P00481481 as photocopy at MO-2692713!, US-2515396 image!).

Nomenclatural note. Even though the original description of *Tynanthus micranthus* does not mention a type specimen, it does cite Correia de Mello as the source of the name. In a contemporaneous treatment Bureau and Schumann (1896) listed two specimens, one of which is a collection by Correia de Mello and here presumed to represent the type. The type is presumably at P, where Bureau worked, and where there are several duplicates of this collection; the best flowering specimen at P is here chosen as the lectotype. A duplicate of this collection may have been deposited at B also, but if so it has been destroyed and no such specimen is documented by the F type photos.

Habitat and distribution. This species is found in humid forest vegetation in Paraguay, Brazil (Mato Grosso do Sul, Paraná, São Paulo), and Argentina (Misiones).

10. Tynanthus panurensis (Bureau) Sandwith, Kew Bull. 8(4): 465. 1953 [1954]. *Schizopsis panurensis* Bureau, Adansonia 5: 373. 1865. TYPE: Brazil. Amazonas: near Panuré at Rio Uaupés, Oct. 1852–Jan. 1853, *R. Spruce 2626* (holotype, P [barcode] P00468600!; isotype, BM!, BM as photocopy at MO-2300302!).

Habitat and distribution. This species is found in humid forest vegetation in Colombia (Amazonas, Caquetá, Putumayo), Ecuador, Peru (Amazonas, Loreto, Pasco, San Martín), Bolivia, and Brazil (Amazonas).

11. Tynanthus polyanthus (Bureau) Sandwith, Kew Bull. 8(4): 465. 1953 [1954]. *Schizopsis polyantha* Bureau, Adansonia 5: 378. 1865. TYPE: Peru. San Martín: Tarapoto, 1855–1856, *R. Spruce 4895* (lectotype, designated here, P [barcode] P00481492!; isolectotypes, C not seen, C as photo F neg. 22126 at MO-1693114!, F-875569 image!, K [barcode] K000202056!, K [barcode] K000202057!, K [barcode] K000202058!, K [barcode] K000202059!, NY [barcode] NY00328924!, P [barcode] P00481493!, P [barcode] P00481494!).

Nomenclatural note. Original material of the type collection is deposited at P, where Bureau worked. Three duplicates are deposited there, and the best material is here selected as the lectotype.

Habitat and distribution. This species is found in humid forest vegetation in the Greater Antilles (Dominican Republic, Puerto Rico), Colombia (Antioquia, Chocó, Meta), Venezuela (Amazonas), Guyana, Ecuador, Peru (Amazonas, Cusco, Huánuco, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Pará).

12. Tynanthus pubescens A. H. Gentry, Mem. New York Bot. Gard. 29(1): 275, fig. 124C. 1978. TYPE: Guyana. Upper Mazaruni River Basin, Kamarang River, Singh line from Akapai to Eboropu escarpment, 500 m, 13 Oct. 1960, *S. S. Tillett & C. L. Tillett* 45643 (holotype, MO-2242100!; isotypes, K!, NY [barcode] NY00328985!, US-2819584 image!).

Habitat and distribution. This species is found in humid forest vegetation in Venezuela (Amazonas), Guyana, Suriname, French Guiana, Peru (San Martín), and Brazil (Pará, Rondônia).

13. Tynanthus sastrei A. H. Gentry, Phytologia 46(4): 214. 1980. TYPE: French Guiana. Sinnamary, on way to Ste. Elie, 23 Sep. 1977, *C. Sastre 6015* (holotype, MO-2630185!; isotypes, P [barcode] P00481495!, P [barcode] P00481496!).

Habitat and distribution. This species is found in humid forest vegetation in Suriname and French Guiana.

14. Tynanthus schumannianus (Kuntze) A. H. Gentry, Ann. Missouri Bot. Gard. 61(3): 874. 1974. *Cuspidaria schumanniana* Kuntze, Revis. Gen. Pl. 3(3): 243. 1893. TYPE: Bolivia. Yacapari, June 1892, *C. E. O. Kuntze s.n.* (holotype, NY [barcode] NY00328766!).

Habitat and distribution. This species is found in humid forest vegetation in Ecuador, Peru (Cusco, Madre de Dios, Puno), Bolivia, and Brazil (Acre, Amazonas, Pará, Rondônia).

15. Tynanthus villosus A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 60, fig. 5. 1976, as "*Tynnathus*." TYPE: Peru. San Martín: Mariscal Cáceres, Tocache Nuevo, Quebrada de Cañuto,

400 m, 18 Aug. 1973, *J. Schunke Vigo 6852* (holotype, MO-2175155!; isotypes, F-1763392 image!, K!, RB-185816 [barcode] 536855!, RB-185816 [barcode] 536925!).

Habitat and distribution. This species is found in humid forest vegetation in Peru (Huánuco, San Martín, Ucayali), Bolivia, and Brazil (Acre).

XXI. Xylophragma Sprague, Hooker's Icon. Pl. 28, tab. 2770. 1905. TYPE: *Xylophragma pratense* (Bureau & K. Schum.) Sprague (lectotype, designated by Gentry [1973b: 997]).

Orthotheca Pichon, Bull. Soc. Bot. France 92: 226. 1946, nom illeg., non *Orthotheca* Brid. (1826). *Heterocalycium* Rauschert, Taxon 31: 558. 1982, replacement name. TYPE: *Heterocalycium heterocalyx* (Bureau & K. Schum.) Raeuschert [≡ *Xylophragma heterocalyx* (Bureau & K. Schum.) A. H. Gentry].

Rojasiophyton Hassl., Repert. Spec. Nov. Regni Veg. 9: 53 1910. TYPE: *Rojasiophyton tuberculatum* Hassl. [= *Xylophragma pratense* (Bureau & K. Schum.) Sprague].

Shrubs, without dimorphic juvenile growth, without strong odor; stems with 4 phloem wedges in cross-section, pith solid; branchlets cylindrical, pubescent, with sparse lenticels, with interpetiolar glands, with discontinuous interpetiolar ridge, with epidermis not peeling; prophylls of axillary buds minute or bromeliad-like, without glands. Leaves (1-) 2- to 3-(5-)foliolate, terminal leaflet often replaced by a simple tendril, tendrils without adhesive disks, without uncinate apices; leaflets with glands sparsely distributed over lamina, without pellucid punctations, with domatia, petiolules not articulated; petiole cylindrical, never modified into a tendril, not articulated. Inflorescence terminal and/or axillary, a compound thyrse. Flowers zygomorphic, pentamerous; calyx cupular, shortly 5-lobed or truncate, coriaceous, villose externally, with glands clustered near margins; corolla pink or magenta, without nectar guides, infundibuliform, straight in tube, membranaceous, villose externally, without glands, lobes 5, imbricate; stamens 4, with well-developed filaments, included, anthers glabrous, thecae straight, pollen in monads, colpate, with exine psilate; ovary sessile, smooth and lepidote externally, ovules in multiple series on each placenta, stigma rhombic, glabrous; disk annular. Capsules linear, flattened, straight, coriaceous or woody, with valves 2, glabrous or puberulous, with or without lenticels, with or without glands, without wings, smooth, with calyx caducous; seeds winged, with body rough and glabrous, wings hyaline or opaque, linear.

Number of species, distribution, and habitat. *Xylophragma* includes seven species found in wet to dry forest, caatinga, and cerrado vegetation from Mexico to Paraguay and southeastern Brazil.

Xylophragma is characterized by the combination of the bromeliad-like prophylls of the axillary buds, 1- to 5-foliolate leaves, simple tendrils, interpetiolar glands, ovules arranged in multiple series on each placenta, and seeds with a rough body (this last character is a synapomorphy of the genus). *Xylophragma* is very similar to *Fridericia* and *Cuspidaria*, which can be separated reliably only by the arrangement of the ovules: in a single series on each placenta in *Fridericia*, and in two series in *Cuspidaria*.

1. Xylophragma harleyi (A. H. Gentry ex M. M. Silva & L. P. Queiroz) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea harleyi* A. H. Gentry ex M. M. Silva & L. P. Queiroz, Sitientibus, Ciênc. Biol. 1: 47. 2001. *Xylophragma harleyi* (A. H. Gentry ex M. M. Silva & L. P. Quieroz) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 772. 2010, nom. nud. invalid. TYPE: Brazil. Bahia: Serra do Curral Feio, 3 km NW of Lagoinha (5.5 km SW of Delfino) on side rd. to Minas do Mimoso, 640 m, 10°27′S, 41°16′W, 5 Mar. 1974, *R. M. Harley, S. A. Renvoize, C. M. Erskine, C. A. Brighton & R. Pinheiro 16736* (holotype, K!; isotypes, MO-2242920!, NY [barcode] NY00313095!, P [barcode] P00468567!).

Habitat and distribution. This species is found in dry caatinga vegetation in eastern Brazil (Bahia, Ceará, Espírito Santo, Minas Gerais, Piauí).

2. Xylophragma heterocalyx (Bureau & K. Schum.) A. H. Gentry, Ann. Missouri Bot. Gard. 66(4): 778. 1979 [1980]. *Saldanhaea heterocalyx* Bureau & K. Schum., Fl. Bras. 8(2): 254. 1896 [1897]. *Orthotheca heterocalyx* (Bureau & K. Schum) Pichon, Bull. Soc. Bot. France 92: 226. 1946. *Heterocalycium heterocalyx* (Bureau & K. Schum.) Rauschert, Taxon 31: 558. 1982. TYPE: Brazil. Rio de Janeiro, 1882, *A. Glaziou 14109* (lectotype, designated here, P [barcode] P00481559!, P [barcode] P00481559 as photocopy at MO-2909930!; isolectotypes, C not seen, C as photo F neg. 22116 at MO-1693050!, K [no #]!, K [no #] as photocopy at MO-2904323!, P [barcode] P00481560!, P [barcode] P00481560 as photocopy at MO-2909930!).

Nomenclatural note. Gentry annotated the two P specimens as the lectotype and isolectotype, respec-

tively, but did not publish this selection. The lectotype is designated here following his annotations.

Habitat and distribution. This species is found in cerrado vegetation in eastern Brazil (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro).

3. **Xylophragma myrianthum** (Cham.) Sprague, Hooker's Icon. Pl. 28: tab. 2770. 1905. *Bignonia myriantha* Cham., Linnaea 7: 684. 1832 [1833]. *Saldanhaea myriantha* (Cham.) Bureau, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1893: 104. 1893 [1894]. TYPE: Brazil. s. loc., 1840, *F. Sellow s.n.* (holotype, LE not seen; isotypes, B†, G-DC!, K!).

Habitat and distribution. This species is found in cerrado vegetation in eastern Brazil (Ceará, Distrito Federal, Espírito Santo, Goiás, Maranhão, Minas Gerais, Paraná, Piauí, Rio de Janeiro, São Paulo, Tocantins).

4. **Xylophragma platyphyllum** (DC.) L. G. Lohmann, comb. nov. Basionym: *Arrabidaea platyphylla* DC., in A. DC., Prodr. 9: 186. 1845. *Petastoma platyphyllum* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 195. 1863. *Xylophragma platyphyllum* (DC.) L. G. Lohmann, Cat. Pl. Fung. Brasil 1: 772. 2010, nom. nud. invalid. TYPE: Brazil. Mato Grosso: Cuiabá, 1832, *A. S. Manso s.n.* (holotype, G-DC!).

Habitat and distribution. This species is found in humid forest vegetation in Peru (Huánuco, Madre de Dios, Ucayali), Bolivia, and Brazil (Acre, Amazonas, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Pará, Rondônia).

5. **Xylophragma pratense** (Bureau & K. Schum.) Sprague, Hooker's Icon. Pl. 28: tab. 2770. 1903. *Tecoma pratensis* Bureau & K. Schum., Nat. Pflazenfam. 4(3b): 238. 1894, nom. nud. invalid. *Saldanhaea pratensis* Bureau & K. Schum., Fl. Bras. 8(2): 256. 1896 [1897]. TYPE: Peru. San Martín: Tarapoto, 1855–1856, *R. Spruce 4232* (lectotype, designated here, K [barcode] K000449744!; isolectotypes, K [barcode] K000449743!, W!).

Nomenclatural note. The name *Tecoma pratensis* was listed by Schumann (1894) in a key that serves as the diagnosis for most of the species that are first described there. However, *T. pratensis* was keyed there together with another species, *T. amazonica* Bureau & K. Schum., and these two species were not distinguished from each other further. Thus, these two names both lack an individual diagnosis and are not validly published. The name *T. pratensis* was later referenced in the description of *Saldanhaea pratensis* Bureau & K. Schum., connecting the identity of these plants but not publishing a combination in *Saldanhaea* (as some authors have supposed) because the name intended as the basionym was never validly published. Two syntypes were cited in the protologue of *S. pratensis*, *Spruce 4232* and *Poeppig 2316* (W not seen, W as photo F neg. 52875 at MO-1693053!). The more widely distributed collection is here chosen as the type, and the best quality flowering specimen, deposited at P where Bureau worked, is designated as the lectotype.

Habitat and distribution. This species is found in humid forest vegetation in Colombia (Amazonas), Peru (Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martín, Ucayali), Bolivia, Paraguay, and Brazil (Acre, Amazonas, Distrito Federal, Goiás, Maranhão, Mato Grosso do Sul, Pará).

6. **Xylophragma seemannianum** (Kuntze) Sandwith, Kew Bull. 8(4): 469. 1953 [1954]. *Saldanhaea seemanniana* Kuntze, Rev. Gen. Pl. 2: 480. 1891, as "*Soldanhaea Seemanniana*." TYPE: Trinidad, Apr. 1975, *C. E. O. Kuntze 744* (lectotype, designated by Gentry [1982: 209], NY [barcode] NY00328923 image!).

Nomenclatural note. The protologue of this name documented it with several elements: a citation of the locality "Trinidad" without a particular specimen noted; a citation of the plants from Gorgona, Colombia, and perhaps also those from Panama that Seemann (1852–1857) incorrectly identified as *Bignonia dentata* A. DC. [a synonym of *Stizophyllum perforatum* (Cham.) Miers]; the specimens *Seemann 179* and *Seemann 603*, without mention of where they were collected or deposited; and the specimen *Jürgensen s.n.* from Colombia at K. A specimen at NY from Trinidad collected by Kuntze appears to represent part of the original material, and was designated by Gentry (1982) as the lectotype.

Habitat and distribution. This species is found in semideciduous to deciduous lowland forest vegetation (Gentry, 1997) in Mexico (Campeche, Chiapas, Colima, Jalisco, Michoacán, Oaxaca, Tabasco, Veracruz), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Bolívar, Boyacá, César, Chocó, Cundinamarca, Magdalena, Meta, Vichada), Venezuela (Amazonas), Trinidad and Tobago, Bolivia, Guyana, Suriname, Peru (Madre de Dios), and northern Brazil (Roraima).

7. Xylophragma unifoliolatum J. F. Morales & Q. Jiménez, Caldasia 31(2): 247. 2009. TYPE: Costa Rica. Guanacaste: Parque Nacional Guanacaste, Cerro El Hacha, camino a Santa Cecilia, 300–600 m, 23 Mar. 1992, *R. Espinoza 250* (holotype, INB not seen; isotypes, CR not seen, MO-5096617 image!).

Habitat and distribution. This species is found in dry forest vegetation in northwestern Costa Rica.

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Appendix 1. List of names lectotypified and neotypified here.

Genus Names with Lectotypes

Periarrabidaea A. Samp.

Species Names with Lectotypes (Only Basionyms Listed)

Adenocalymma bracteolatum DC.
Adenocalymma bullatum Bureau ex K. Schum.
Adenocalymma flavum Mart. ex DC.
Adenocalymma heterophyllum Kraenzl.
Adenocalymma inundatum Mart. ex DC.
Adenocalymma magnificum Mart. ex DC.
Adenocalymma nervosum Bureau & K. Schum.
Adenocalymma paulistarum Bureau ex K. Schum.
Adenocalymma scabriusculum Mart. ex DC.
Adenocalymma uleanum Kraenzl.
Amphilophium pubescens Spreng.
Anemopaegma album Mart. ex DC.
Anemopaegma citrinum Mart. ex DC.
Anemopaegma glaucum Mart. ex DC.
Anemopaegma goyazense K. Schum.
Anemopaegma jucundum Bureau & K. Schum.
Anemopagema paraense Bureau & K. Schum.
Anemopaegma parkeri Sprague
Anemopaegma velutinum Mart. ex DC.
Arrabidaea celastroides Bureau ex K. Schum.
Arrabidaea cinerea Bureau & K. Schum.
Arrabidaea claussenii A. DC.
Arrabidaea dispar Bureau ex K. Schum.
Arrabidaea egensis Bureau & K. Schum.
Arrabidaea florida DC.
Arrabidaea lauta Bureau & K. Schum.
Arrabidaea mutabilis Bureau & K. Schum.
Arrabidaea nicotianiflora Kraenzl.
Arrabidaea subexserta Bureau & K. Schum.
Bignonia arvensis Vell.
Bignonia chamberlaynii Sims
Bignonia conjugata Vell.
Bignonia convoluta Vell.
Bignonia cordata Vell.
Bignonia elegans Vell.
Bignonia erubescens DC.
Bignonia fasciculata Vell.
Bignonia flavida DC.
Bignonia fluminensis Vell.
Bignonia grandifolia Jacq.
Bignonia impressa Rusby
Bignonia latifolia Rich.
Bignonia longa Vell.
Bignonia longiflora Cav.
Bignonia pedunculata Vell.
Bignonia perianthomega Vell.
Bignonia quadrivalvis Jacq.
Bignonia rego Vell.
Bignonia scandens Vell.
Bignonia selloi Spreng.
Bignonia ternata Vell.
Bignonia tetragonoloba Jacq.
Bignonia unguiculata Vell.
Clytostoma convolvuloides Bureau & K. Schum.
Clytostoma costatum Bureau & K. Schum.
Clytostoma pterocalyx Sprague ex Urb.
Cremastus lachnaeus Bureau
Cuspidaria multiflora DC.
Distictis crassa Bureau & K. Schum.
Fridericia speciosa Mart.
Glaziova bauhinioides Bureau ex Baill.
Lundia densiflora DC.
Lundia obliqua Sond.
Lundia virginalis DC.
Macfadyena dentata K. Schum.
Mansoa glaziovii Bureau & K. Schum.
Memora axillaris K. Schum.
Paramansoa grosourdyana Baill.
Petastoma formosum Bureau
Pithecoctenium parviflorum Mart. ex DC.
Pleonotoma stichadenia K. Schum.
Pseudopaegma colombianum Sandwith
Saldanhaea costaricensis Kraenzl.
Saldanhaea heterocalyx Bureau & K. Schum.
Saldanhaea pratensis Bureau & K. Schum.
Schizopsis polyantha Bureau
Setilobus bracteatus Baill. ex Bureau & K. Schum.
Tecoma lateriflora Mart.
Tynanthus micranthus Corr. Méllo ex K. Schum.

Species Name with Neotypes (Only Basionym Listed)

Memora campicola Pilg.

Appendix 2. Index to names treated in this classification.

Plant names in boldface are **accepted** species of Bignoniaceae tribe Bignonieae, according to the taxonomic treatment here. Names in italics are *synonyms*, with the accepted name

indicated by "=". The names included in this appendix all correspond to the tribe Bignonieae and to names treated in this article. These names include all accepted genera, all generic synonyms and their type species, all accepted names in the manuscript, and the homotypic names that correspond to the accepted names as follows. For the homotypic names of accepted names, all validly published names are included, with selected significant orthographic variants and selected significant invalid names. The index does not list all the invalid names mentioned in the article, only the ones that have generated confusion. The status of the individual names (for example, invalid or illegitimate) is not marked here; see the taxonomic treatment for information about this. Names lectotypified or neotypified here are indicated by double asterisks (**). Genera listed here in brackets are not included in the tribe Bignonieae, but are mentioned in this list because some species of Bignonieae were (erroneously) classified in those genera. Additional synonymous names for Bignonieae can be found at <http://www.iplants.org> and <http://www.TROPICOS.org>.

Adenocalymma Mart. ex Meisn.
Adenocalymma adnophorum (Sandwith) L. G. Lohmann
Adenocalymma album (Aubl.) L. G. Lohmann
Adenocalymma allamandiflorum (Bureau ex K. Schum.) L. G. Lohmann
Adenocalymma alliaceum (Lam.) Miers, = **Mansoa alliacea** (Lam.) A. H. Gentry
Adenocalymma apparicianum J. C. Gomes
Adenocalymma apurense (Kunth) Sandwith
Adenocalymma arthropetiolatum A. H. Gentry
Adenocalymma aspericarpum (A. H. Gentry) L. G. Lohmann
Adenocalymma axillare (K. Schum.) L. G. Lohmann
Adenocalymma bilabiatum (Sprague) Sandwith, = **Tanaecium bilabiatum** (Sprague) L. G. Lohmann
Adenocalymma bipinnatum (S. Moore) L. G. Lohmann
Adenocalymma biternatum (A. Samp.) L. G. Lohmann
Adenocalymma bracteatum (Cham.) DC.
Adenocalymma bracteolatum DC.**
Adenocalymma bracteosum (DC.) L. G. Lohmann
Adenocalymma bullatum Bureau ex K. Schum.**
Adenocalymma calcareum Udulutsch & P. Dias
Adenocalymma campicola (Pilg.) L. G. Lohmann
Adenocalymma chocoense A. H. Gentry
Adenocalymma cidii (A. H. Gentry ex Hauk) L. G. Lohmann
Adenocalymma cladotrichum (Sandwith) L. G. Lohmann
Adenocalymma comosum (Cham.) DC.
Adenocalymma contractum (A. H. Gentry ex Hauk) L. G. Lohmann
Adenocalymma coriaceum A. DC.
Adenocalymma cristacalyx (A. H. Gentry) L. G. Lohmann
Adenocalymma croatii (A. H. Gentry) L. G. Lohmann
Adenocalymma cymbalum (Cham.) Bureau & K. Schum.
Adenocalymma dichilum A. H. Gentry
Adenocalymma divaricatum Miers
Adenocalymma dugandii Sandwith
Adenocalymma dusenii Kraenzl.
Adenocalymma elegans (Vell.) Mart. ex K. Schum., = **Fridericia elegans** (Vell.) L. G. Lohmann
Adenocalymma flavidum (DC.) L. G. Lohmann, = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Adenocalymma flavidum Miers, identity unclear
Adenocalymma flaviflorum (Miq.) L. G. Lohmann
Adenocalymma flavum Mart. ex DC.**
Adenocalymma floribundum DC., = **Cuspidaria floribunda** (DC.) A. H. Gentry
Adenocalymma fruticosum A. H. Gentry
Adenocalymma gracielzae A. H. Gentry
Adenocalymma grandifolium Mart. ex DC.
Adenocalymma hatschbachii A. H. Gentry
Adenocalymma heterophyllum Kraenzl.**
Adenocalymma hirtum (Mart. ex DC.) Bureau & K. Schum.
Adenocalymma hypostictum Bureau & K. Schum.
Adenocalymma imperatoris-maximilianii (Wawra) L. G. Lohmann
Adenocalymma impressum (Rusby) Sandwith
Adenocalymma inundatum Mart. ex DC.**
Adenocalymma involucratum (Bureau & K. Schum.) L. G. Lohmann
Adenocalymma juliae (A. H. Gentry) L. G. Lohmann
Adenocalymma kerere (Aubl.) Bureau & K. Schum., = **Pachyptera kerere** (Aubl.) Sandwith
Adenocalymma longilineum (A. Samp.) L. G. Lohmann
Adenocalymma madgalenense Dugand
Adenocalymma magnificum Mart. ex DC.**
Adenocalymma magnoalatum Scud.
Adenocalymma marginatum (Cham.) DC.
Adenocalymma molle (A. H. Gentry) L. G. Lohmann
Adenocalymma moringifolium (DC.) L. G. Lohmann
Adenocalymma neoflavidum L. G. Lohmann, = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Adenocalymma nervosum Bureau & K. Schum.**
Adenocalymma nodosum (Silva Manso) L. G. Lohmann
Adenocalymma patulum (Miers) L. G. Lohmann
Adenocalymma paucifoliolatum (A. H. Gentry) L. G. Lohmann
Adenocalymma paulistarum Bureau ex K. Schum.**
Adenocalymma pedunculatum (Vell.) L. G. Lohmann
Adenocalymma peregrinum (Miers) L. G. Lohmann
Adenocalymma pliciflorum Mart. ex DC., = **Fridericia pliciflora** (Mart. ex DC.) L. G. Lohmann
Adenocalymma prancei A. H. Gentry
Adenocalymma prasinum Miers, = **Adenocalyma grandifolium** Mart. ex DC.
Adenocalymma pseudopatulum (A. H. Gentry) L. G. Lohmann
Adenocalymma pubescens (Spreng.) L. G. Lohmann
Adenocalymma purpurascens Rusby
Adenocalymma racemosum (A. H. Gentry) L. G. Lohmann
Adenocalymma reticulatum Bureau ex K. Schum.
Adenocalymma salmoneum J. C. Gomes
Adenocalymma salzmannii DC.
Adenocalymma sastrei (A. H. Gentry ex Hauk) L. G. Lohmann
Adenocalymma saulense A. H. Gentry
Adenocalymma scabriusculum Mart. ex DC.**
Adenocalymma scansile Miers
Adenocalymma schomburgkii (DC.) L. G. Lohmann
Adenocalymma sousae A. H. Gentry
Adenocalymma subincaum Huber
Adenocalymma subsessilifolium DC.
Adenocalymma subspicatum A. H. Gentry
Adenocalymma tanaeciicarpum (A. H. Gentry) L. G. Lohmann
Adenocalymma ternatum (Vell.) Corr. Méllo ex Bureau & K. Schum.
Adenocalymma trichocladum (DC.) L. G. Lohmann
Adenocalymma trifoliatum (Vell.) R. C. Laroche
Adenocalymma ubatubense Assis & Semir
Adenocalymma uleanum Kraenzl.**
Adenocalymma validum (K. Schum.) L. G. Lohmann
Adenocalymma velutinum (A. H. Gentry ex Hauk) L. G. Lohmann
Adenocalymma verruciferum (Schltdl.) Miers, = **Mansoa verrucifera** (Schltdl.) A. H. Gentry

Adenocalymma verrucosum Standl., = **Fridericia schumanniana** (Loes.) L. G. Lohmann
Alsocydia DC. ex J. C. Gomes, = **Fridericia** Mart.
Alsocydia erubescens (DC.) J. C. Gomes, = **Fridericia erubescens** (DC.) L. G. Lohmann
Amphilophium Kunth
Amphilophium arenarium (A. H. Gentry) L. G. Lohmann
Amphilophium aschersonii Ule
Amphilophium bauhinioides (Bureau ex Baill.) L. G. Lohmann
Amphilophium blanchetii (DC.) Bureau & K. Schum.
Amphilophium bracteatum (Cham.) L. G. Lohmann
Amphilophium buccinatorium (DC.) L. G. Lohmann
Amphilophium campinae (A. Samp.) L. G. Lohmann
Amphilophium carolinae (Lindl.) L. G. Lohmann
Amphilophium chocoense (A. H. Gentry) L. G. Lohmann
Amphilophium cremersii (A. H. Gentry) L. G. Lohmann
Amphilophium crucigerum (L.) L. G. Lohmann
Amphilophium cuneifolium (DC.) L. G. Lohmann
Amphilophium cynanchoides (DC.) L. G. Lohmann, = **Amphilophium carolinae** (Lindl.) L. G. Lohmann
Amphilophium dasytrichum (Sandwith) L. G. Lohmann
Amphilophium dolichoides (Cham.) L. G. Lohmann
Amphilophium dusenianum (Kraenzl.) L. G. Lohmann
Amphilophium ecuadorense A. H. Gentry
Amphilophium elongatum (Vahl) L. G. Lohmann
Amphilophium falcatum (Vell.) L. G. Lohmann
Amphilophium frutescens (DC.) L. G. Lohmann
Amphilophium glaziovii Bureau ex K. Schum.
Amphilophium gnaphalanthum (A. Rich.) L. G. Lohmann
Amphilophium granulosum (Bureau & K. Schum.) L. G. Lohmann
Amphilophium lactiflorum (Vahl) L. G. Lohmann
Amphilophium laeve (Sandwith) L. G. Lohmann
Amphilophium laxiflorum (DC.) L. G. Lohmann
Amphilophium lohmanniae (A. Pool) L. G. Lohmann
Amphilophium magnoliifolium (Kunth) L. G. Lohmann
Amphilophium mansoanum (DC.) L. G. Lohmann
Amphilophium monophyllum (Sandwith) L. G. Lohmann
Amphilophium neoglaziovii L. G. Lohmann, = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Amphilophium nunezii (A. H. Gentry) L. G. Lohmann
Amphilophium obovatum (Sandwith) L. G. Lohmann
Amphilophium occidentale (A. H. Gentry) L. G. Lohmann
Amphilophium paniculatum (L.) Kunth
Amphilophium pannosum (DC.) Bureau & K. Schum.
Amphilophium parkeri (DC.) L. G. Lohmann
Amphilophium pauciflorum (A. H. Gentry) L. G. Lohmann
Amphilophium perbracteaum A. H. Gentry
Amphilophium pilosum Standl.
Amphilophium porphyrotrichum (Sandwith) L. G. Lohmann
Amphilophium pubescens Spreng.**, = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Amphilophium pulverulentum (Sandwith) L. G. Lohmann
Amphilophium racemosum (Bureau & K. Schum.) L. G. Lohmann
Amphilophium reticulatum (A. H. Gentry) L. G. Lohmann
Amphilophium rodriguesii (A. H. Gentry) L. G. Lohmann
Amphilophium sandwithii Fabris
Amphilophium scabriusculum (Mart. ex DC.) L. G. Lohmann
Amphilophium stamineum (Lam.) L. G. Lohmann
Amphilophium steyermarkii (A. H. Gentry) L. G. Lohmann
Anemopaegma Mart. ex Meisn.
Anemopaegma acutifolium DC.
Anemopaegma alatum A. H. Gentry
Anemopaegma album Mart. ex DC.**
Anemopaegma arvense (Vell.) Stellfeld ex J. F. Souza
Anemopaegma brevipes S. Moore
Anemopaegma chamberlaynii (Sims) Bureau & K. Schum.
Anemopaegma chrysanthum Dugand
Anemopaegma chrysoleucum (Kunth) Sandwith
Anemopaegma citrinum Mart. ex DC.**
Anemopaegma colombianum (Sandwith) A. H. Gentry
Anemopaegma decorum S. Moore, = **Bignonia decora** (S. Moore) L. G. Lohmann
Anemopaegma flavum Morong
Anemopaegma floridum Mart. ex DC.
Anemopaegma foetidum Bureau & K. Schum.
Anemopaegma glaucum Mart. ex DC.**
Anemopaegma goyazense K. Schum.**
Anemopaegma gracile Bureau & K. Schum.
Anemopaegma grandifolium (Jacq.) Merr. & Sandwith
Anemopaegma granvillei A. H. Gentry
Anemopaegma heringeri J. C. Gomes
Anemopaegma hilarianum Bureau & K. Schum.
Anemopaegma insculptum (Sandwith) A. H. Gentry
Anemopaegma ionanthum A. H. Gentry
Anemopaegma jucundum Bureau & K. Schum.**
Anemopaegma karstenii Bureau & K. Schum.
Anemopaegma laeve DC.
Anemopaegma lanceolatum (DC.) Bureau ex K. Schum., = **Mansoa lanceolata** (DC.) A. H. Gentry
Anemopaegma longidens Mart. ex DC.
Anemopaegma longipetiolatum Sprague
Anemopaegma microcalyx (G. Mey.) Bureau & K. Schum., = **Bignonia microcalyx** G. Mey.
Anemopaegma mirandum (Cham.) Mart. ex DC., = **Anemopaegma arvense** (Vell.) Stellfeld ex J. F. Souza
Anemopaegma mirabile (Sandwith) A. H. Gentry
Anemopaegma oligoneuron (Sprague & Sandwith) A. H. Gentry
Anemopaegma orbiculatum (Jacq.) DC.
Anemopaegma pabstii A. H. Gentry
Anemopaegma pachyphyllum Bureau & K. Schum.
Anemopaegma paraense Bureau & K. Schum.**
Anemopaegma parkeri Sprague**
Anemopaegma patelliforme A. H. Gentry
Anemopaegma poeppigii DC., = **Fridericia poeppigii** (DC.) L. G. Lohmann
Anemopaegma prostratum DC.
Anemopaegma puberulum (Seibert) Miranda
Anemopaegma robustum Bureau & K. Schum.
Anemopaegma rugosum (Schltdl.) Sprague
Anemopaegma salicifolium (Kunth) Sandwith
Anemopaegma santaritense A. H. Gentry
Anemopaegma scabriusculum Mart. ex DC.
Anemopaegma scandens (Vell.) Corr. Méllo ex K. Schum., = **Anemopaegma chamberlaynii** (Sims) Bureau & K. Schum.
Anemopaegma setilobum A. H. Gentry
Anemopaegma velutinum Mart. ex DC.**
Anemopaegma villosum A. H. Gentry
Anemopaegma whitei Rusby, = **Fridericia whitei** (Rusby) L. G. Lohmann
Anisostichus Bureau, = **Bignonia** L.
Anisostichus capreolata (L.) Bureau, = **Bignonia capreolata** L.
Anisostichus crucigera (L.) Bureau ex Small, = **Amphilophium crucigerum** (L.) L. G. Lohmann
Anomoctenium Pichon, = **Amphilophium** Kunth
Anomoctenium granulosum (Bureau & K. Schum.) Sandwith, = **Amphilophium granulosum** (Bureau & K. Schum.) L. G. Lohmann

Anomoctenium stipulare (Mart. ex DC.) Pichon, = **Amphilophium frutescens** (DC.) L. G. Lohmann
Arrabidaea DC., = **Fridericia** Mart.
Arrabidaea sect. *Paracarpaea* K. Schum., = **Fridericia** Mart.
Arrabidaea affinis A. H. Gentry, = **Tanaecium affine** (A. H. Gentry) L. G. Lohmann
Arrabidaea argentea Wawra, = **Cuspidaria argentea** (Wawra) Sandwith
Arrabidaea arthrerion (Mart.) Bureau ex K. Schum., = **Fridericia arthrerion** (Mart.) L. G. Lohmann
Arrabidaea bahiensis (Schauer ex DC.) Sandwith & Moldenke, = **Fridericia bahiensis** (Schauer ex DC.) L. G. Lohmann
Arrabidaea bilabiata (Sprague) Sandwith, = **Tanaecium bilabiatum** (Sprague) L. G. Lohmann
Arrabidaea brachypoda Bureau, = **Fridericia platyphylla** (Cham.) L. G. Lohmann
Arrabidaea bracteolata (DC.) Sandwith, = **Fridericia bracteolata** (DC.) L. G. Lohmann
Arrabidaea candicans (Rich.) DC., = **Fridericia candicans** (Rich.) L. G. Lohmann
Arrabidaea carichanensis (Kunth) Bureau & K. Schum., = **Fridericia carichanensis** (Kunth) L. G. Lohmann
Arrabidaea caudigera (S. Moore) A. H. Gentry, = **Fridericia caudigera** (S. Moore) L. G. Lohmann
Arrabidaea celastroides Bureau ex K. Schum.**, = **Fridericia celastroides** (Bureau ex K. Schum.) L. G. Lohmann
Arrabidaea chica (Bonpl.) Verl., = **Fridericia chica** (Bonpl.) L. G. Lohmann
Arrabidaea chica var. *viscida* Donn. Sm., = **Fridericia viscida** (Donn. Sm.) L. G. Lohmann
Arrabidaea cinerea Bureau ex K. Schum.**, = **Fridericia cinerea** (Bureau ex K. Schum.) L. G. Lohmann
Arrabidaea cinnamomea (DC.) Sandwith, = **Fridericia cinnamomea** (DC.) L. G. Lohmann
Arrabidaea claussenii A. DC.**, = **Fridericia claussenii** (A. DC.) L. G. Lohmann
Arrabidaea conjugata (Vell.) Mart., = **Fridericia conjugata** (Vell.) L. G. Lohmann
Arrabidaea corallina (Jacq.) Sandwith, = **Fridericia dichotoma** (Jacq.) L. G. Lohmann
Arrabidaea corchoroides (Cham.) DC., = **Fridericia corchoroides** (Cham.) L. G. Lohmann
Arrabidaea corymbifera (Vahl) Bureau ex K. Schum., = **Lundia corymbifera** (Vahl) Sandwith
Arrabidaea costaricensis (Kraenzl.) A. H. Gentry, = **Fridericia costaricensis** (Kraenzl.) L. G. Lohmann
Arrabidaea crassa (Bureau & K. Schum.) Sprague, = **Fridericia crassa** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea craterophora (DC.) Bureau, = **Fridericia craterophora** (DC.) L. G. Lohmann
Arrabidaea cuneifolia (DC.) Sandwith, = **Fridericia cuneifolia** (DC.) L. G. Lohmann
Arrabidaea decora (S. Moore) Hassl., = **Bignonia decora** (S. Moore) L. G. Lohmann
Arrabidaea dichotoma Bureau, = **Tanaecium selloi** (Spreng.) L. G. Lohmann
Arrabidaea dispar Bureau ex K. Schum.**, = **Fridericia dispar** (Bureau ex K. Schum.) L. G. Lohmann
Arrabidaea egensis Bureau & K. Schum.**, = **Fridericia egensis** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea elegans (Vell.) A. H. Gentry, = **Fridericia elegans** (Vell.) L. G. Lohmann
Arrabidaea fagoides (Cham.) Bureau, = **Fridericia fagoides** (Cham.) L. G. Lohmann
Arrabidaea fanshawei Sandwith, = **Fridericia fanshawei** (Sandwith) L. G. Lohmann
Arrabidaea fasciculata (Vell.) DC., = **Tynanthus fasciculatus** (Vell.) Miers
Arrabidaea floribunda (Kunth) Loes., = **Fridericia floribunda** (Kunth) L. G. Lohmann
Arrabidaea florida DC.**, = **Fridericia florida** (DC.) L. G. Lohmann
Arrabidaea formosa (Bureau) Sandwith, = **Fridericia formosa** (Bureau) L. G. Lohmann
Arrabidaea grosourdyana (Baill.) Sandwith, = **Fridericia grosourdyana** (Baill.) L. G. Lohmann
Arrabidaea harleyi A. H. Gentry ex M. M. Silva & L. P. Queiroz, = **Xylophragma harleyi** (A. H. Gentry ex M. M. Silva & L. P. Queiroz) L. G. Lohmann
Arrabidaea japurensis (DC.) Bureau & K. Schum., = **Fridericia japurensis** (DC.) L. G. Lohmann
Arrabidaea inaequalis (DC. ex Splitg.) Bureau ex K. Schum., = **Cuspidaria inaequalis** (DC. ex Splitg.) L. G. Lohmann
Arrabidaea lachnaea (Bureau) Sandwith, = **Cuspidaria lachnaea** (Bureau) L. G. Lohmann
Arrabidaea lasiantha Bureau & K. Schum., = **Cuspidaria lasiantha** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea lauta Bureau & K. Schum.**, = **Fridericia lauta** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea leucopogon (Cham.) Sandwith, = **Fridericia leucopogon** (Cham.) L. G. Lohmann
Arrabidaea limae A. H. Gentry, = **Fridericia limae** (A. H. Gentry) L. G. Lohmann
Arrabidaea magnifica (W. Bull) Sprague ex Steenis, = **Bignonia magnifica** W. Bull
Arrabidaea mollis (Vahl) Bureau ex K. Schum., = **Fridericia mollis** (Vahl) L. G. Lohmann
Arrabidaea mollissima (Kunth) Bureau & K. Schum., = **Fridericia mollissima** (Kunth) L. G. Lohmann
Arrabidaea monophylla A. H. Gentry, = **Fridericia monophylla** (A. H. Gentry) L. G. Lohmann
Arrabidaea mutabilis Bureau & K. Schum.**, = **Tanaecium mutabile** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea nicotianiflora Kraenzl.**, = **Fridericia nicotianiflora** (Kraenzl.) L. G. Lohmann
Arrabidaea nigrescens Sandwith, = **Fridericia nigrescens** (Sandwith) L. G. Lohmann
Arrabidaea oligantha Bureau & K. Schum., = **Fridericia oligantha** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea ornithophila A. H. Gentry, = **Fridericia ornithophila** (A. H. Gentry) L. G. Lohmann
Arrabidaea oxycarpa Urb., = **Fridericia oxycarpa** (Urb.) L. G. Lohmann
Arrabidaea paniculata (L.) Seem., = **Amphilophium paniculatum** (L.) Kunth
Arrabidaea paradoxa (Sandwith) Sandwith, = **Fridericia paradoxa** (Sandwith) L. G. Lohmann
Arrabidaea parviflora (Mart. ex DC.) Bureau & K. Schum., = **Fridericia parviflora** (Mart. ex DC.) L. G. Lohmann
Arrabidaea patellifera (Schltdl.) Sandwith, = **Fridericia patellifera** (Schltdl.) L. G. Lohmann
Arrabidaea pearcei (Rusby) K. Schum. ex Urb., = **Fridericia pearcei** (Rusby) L. G. Lohmann
Arrabidaea platyphylla (Cham.) Bureau & K. Schum., = **Fridericia platyphylla** (Cham.) L. G. Lohmann
Arrabidaea platyphylla DC., = **Xylophragma platyphyllum** (DC.) L. G. Lohmann
Arrabidaea pliciflora (Mart. ex DC.) Bureau & K. Schum., = **Fridericia pliciflora** (Mart. ex DC.) L. G. Lohmann
Arrabidaea podopogon (DC.) A. H. Gentry, = **Fridericia podopogon** (DC.) L. G. Lohmann
Arrabidaea poeppigii (DC.) Sandwith, = **Fridericia poeppigii** (DC.) L. G. Lohmann

Arrabidaea potosina K. Schum. & Loes., = **Bignonia potosina** (K. Schum. & Loes.) L. G. Lohmann
Arrabidaea prancei A. H. Gentry, = **Fridericia prancei** (A. H. Gentry) L. G. Lohmann
Arrabidaea puberula (Mart. ex DC.) Bureau, = **Cuspidaria puberula** Mart. ex DC.
Arrabidaea pubescens (L.) A. H. Gentry, = **Fridericia pubescens** (L.) L. G. Lohmann
Arrabidaea pulchella (Cham.) Bureau, = **Cuspidaria pulchella** (Cham.) K. Schum.
Arrabidaea pulchra (Cham.) Sandwith, = **Cuspidaria pulchra** (Cham.) L. G. Lohmann
Arrabidaea rego (Vell.) DC., = **Fridericia rego** (Vell.) L. G. Lohmann
Arrabidaea revillae A. H. Gentry, = **Tanaecium revillae** (A. H. Gentry) L. G. Lohmann
Arrabidaea samydoides (Cham.) Sandwith, = **Fridericia samydoides** (Cham.) L. G. Lohmann
Arrabidaea sceptrum (Cham.) Sandwith, = **Cuspidaria sceptrum** (Cham.) L. G. Lohmann
Arrabidaea sciuripabulum K. Schum., = **Bignonia sciuripabulum** (K. Schum.) L. G. Lohmann
Arrabidaea selloi (Spreng.) Sandwith, = **Tanaecium selloi** (Spreng.) L. G. Lohmann
Arrabidaea simplex A. H. Gentry, = **Fridericia simplex** (A. H. Gentry) L. G. Lohmann
Arribadaea sordida Bureau & K. Schum., = **Bignonia sordida** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea spicata Bureau & K. Schum., = **Fridericia spicata** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea subexserta Bureau & K. Schum.**, = **Fridericia subexserta** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea subincana Mart., = **Fridericia subincana** (Mart.) L. G. Lohmann
Arrabidaea subverticillata Bureau & K. Schum., = **Fridericia subverticillata** (Bureau & K. Schum.) L. G. Lohmann
Arrabideaea trachyphylla (Bureau & K. Schum.) Sandwith, = **Fridericia trachyphylla** (Bureau & K. Schum.) L. G. Lohmann
Arrabidaea trailii Sprague, = **Fridericia trailii** (Sprague) L. G. Lohmann
Arrabidaea trichoclada (DC.) Bureau & K. Schum., = **Adenocalymma trichocladum** (DC.) L. G. Lohmann
Arrabidaea triplinervia (Mart. ex DC.) Baill. ex Bureau, = **Fridericia triplinervia** (Mart. ex DC.) L. G. Lohmann
Arrabidaea truncata (Sprague) Sandwith, = **Fridericia truncata** (Sprague) L. G. Lohmann
Arrabidaea tuberculata DC., = **Fridericia pilulifera** (Rich.) L. G. Lohmann
Arrabidaea tynanthoides A. H. Gentry, = **Fridericia tynanthoides** (A. H. Gentry) L. G. Lohmann
Arrabidaea verrucosa (Standl.) A. H. Gentry, = **Fridericia schumanniana** (Loes.) L. G. Lohmann
Arrabidaea viscida (Donn. Sm.) A. H. Gentry, = **Fridericia viscida** (Donn. Sm.) L. G. Lohmann
Arrabidaea weberbaueri Sprague, = **Cuspidaria weberbaueri** (Sprague) A. H. Gentry
Arrabidaea whitei (Rusby) Sandwith, = **Fridericia whitei** (Rusby) L. G. Lohmann
Arrabidaea xanthophylla (DC.) Bureau & K. Schum., = **Tanaecium xanthophyllum** (DC.) L. G. Lohmann
Batocydia Mart. ex Britton & Wilson, = **Dolichandra** Cham.
Batocydia unguis-cati (L.) Mart. ex Britton, = **Dolichandra unguis-cati** (L.) L. G. Lohmann
Bayonia Dugand, = **Mansoa** DC.
Bayonia helicocalyx (Kuntze) Dugand, = **Mansoa verrucifera** (Schltdl.) A. H. Gentry
Bignonia L.
Bignonia aequinoctialis L.
Bignonia aequinoctialis var. *chamberlaynii* (Sims) Ker Gawl., = **Anemopaegma chamberlaynii** (Sims) Bureau & K. Schum.
Bignonia alba Aubl., = **Adenocalymma album** (Aubl.) L. G. Lohmann
Bignonia albiflora Salzm. ex DC., = **Pleonotoma albiflora** (Salzm. ex DC.) A. H. Gentry
Bignonia alliacea Lam., = **Mansoa alliacea** (Lam.) A. H. Gentry
Bignonia apurensis Kunth, = **Adenocalumma apurense** (Kunth) Sandwith
Bignonia arthrerion Mart., = **Fridericia arthrerion** (Mart.) L. G. Lohmann
Bignonia arvensis Vell.**, = **Anemopaegma arvense** (Vell.) Stellfeld ex J. F. Souza
Bignonia binata Thunb.
Bignonia brachypoda DC., = **Fridericia platyphylla** (Cham.) L. G. Lohmann
Bignonia brachypoda var. *platyphylla* (Cham.) DC., = **Fridericia platyphylla** (Cham.) L. G. Lohmann
Bignonia bracteata Cham., = **Adenocalymma bracteatum** (Cham.) DC.
Bignonia bracteolata DC., = **Fridericia bracteolata** (DC.) L. G. Lohmann
Bignonia bracteomana (K. Schum.) L. G. Lohmann
Bignonia buccinatoria (DC.) Mairet ex Hemsl., = **Amphilophium buccinatorium** (DC.) L. G. Lohmann
Bignonia callistegioides Cham.
Bignonia carolinae Lindl., = **Amphilophium carolinae** (Lindl.) L. G. Lohmann
Bignonia campanulata Cham.
Bignonia candicans Rich., = **Fridericia candicans** (Rich.) L. G. Lohmann
Bignonia capreolata L.
Bignonia carichanensis Kunth, = **Fridericia carichanensis** (Kunth) L. G. Lohmann
Bignonia caudigera S. Moore, = **Fridericia caudigera** (S. Moore) L. G. Lohmann
Bignonia chamberlaynii Sims**, = **Anemopaegma chamberlaynii** (Sims) Bureau & K. Schum.
Bignonia chrysoleuca Kunth, = **Anemopaegma chrysoleucum** (Kunth) Sandwith
Bignonia chica Bonpl., = **Fridericia chica** (Bonpl.) L. G. Lohmann
Bignonia cinnamomea DC., = **Fridericia cinnamomea** (DC.) L. G. Lohmann
Bignonia clematis Kunth, = **Pleonotoma clematis** (Kunth) Miers
Bignonia cognata Cham., = **Tynanthus cognatus** (Cham.) Miers
Bignonia comosa Cham., = **Adenocalymma comosum** (Cham.) DC.
Bignonia conjugata Vell.**, = **Fridericia conjugata** (Vell.) L. G. Lohmann
Bignonia convoluta Vell.**, = **Cuspidaria convoluta** (Vell.) A. H. Gentry
Bignonia convolvuloides (Bureau & K. Schum.) L. G. Lohmann
Bignonia corallina Jacq., = **Fridericia dichotoma** (Jacq.) L. G. Lohmann
Bignonia corchoroides Cham., = **Fridericia corchoroides** (Cham.) L. G. Lohmann
Bignonia cordata Vell.**, = **Lundia corymbifera** (Vahl) Sandwith

Bignonia cordifolia DC. = **Manaosella cordifolia** (DC.) A. H. Gentry
Bignonia corymbifera Vahl = **Lundia corymbifera** (Vahl) Sandwith
Bignonia corymbosa (Vent.) L. G. Lohmann
Bignonia costata (Bureau & K. Schum.) L. G. Lohmann
Bignonia craterophora DC. = **Fridericia craterophora** (DC.) L. G. Lohmann
Bignonia crucigera L., = **Amphilophium crucigerum** (L.) L. G. Lohmann
Bignonia cuneata (Dugand) L. G. Lohmann
Bignonia cuneifolia DC., = **Fridericia cuneifolia** (DC.) L. G. Lohmann
Bignonia cymbalum Cham., = **Adenocalymma cymbalum** (Cham.) Bureau & K. Schum.
Bignonia decora (S. Moore) L. G. Lohmann
Bignonia dichotoma Jacq., = **Fridericia dichotoma** (Jacq.) L. G. Lohmann
Bignonia difficilis Cham., = **Mansoa difficilis** (Cham.) Bureau & K. Schum.
Bignonia diversifolia Kunth
Bignonia dolichoides Cham., = **Amphilophium dolichoides** (Cham.) L. G. Lohmann
Bignonia elegans Cham., = **Tynanthus elegans** Miers
Bignonia elegans Vell.**, = **Fridericia elegans** (Vell.) L. G. Lohmann
Bignonia elongata Vahl, = **Amphilophium elongatum** (Vahl) L. G. Lohmann
Bignonia erubescens DC.**, = **Fridericia erubescens** (DC.) L. G. Lohmann
Bignonia fagoides Cham., = **Fridericia fagoides** (Cham.) L. G. Lohmann
Bignonia falcata Vell., = **Amphilophium falcatum** (Vell.) L. G. Lohmann
Bignonia fallax Cham., = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Bignonia fasciculata Vell.**, = **Tynanthus fasciculatus** (Vell.) Miers
Bignonia flavida DC.**, = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Bignonia floribunda Kunth, = **Fridericia floribunda** (Kunth) L. G. Lohmann
Bignonia fluminensis Vell.**, = **Pleonotoma fluminensis** (Vell.) A. H. Gentry
Bignonia gnaphalantha A. Rich., = **Amphilophium gnaphalanthum** (A. Rich.) L. G. Lohmann
Bignonia grandifolia Jacq.**, = **Anemopaegma grandifolium** (Jacq.) Merr. & Sandwith
Bignonia grandifolia Vell., = **Adenocalymma grandifolium** Mart. ex DC.
Bignonia heterophylla Willd., = **Pachyptera kerere** (Aubl.) Sandwith
Bignonia hyancinthina (Standl.) L. G. Lohmann
Bignonia hymenaea DC., = **Mansoa hymenaea** (DC.) A. H. Gentry
Bignonia imperatoris-maximilianii Wawra, = **Adenocalymma imperatoris-maximilianii** (Wawra) L. G. Lohmann
Bignonia impressa Rusby**, = **Adenocalymma impressum** (Rusby) Sandwith
Bignonia inaequalis DC. ex Splitg., = **Cuspidaria inaequalis** (DC. ex Splitg.) L. G. Lohmann
Bignonia jasminifolia Kunth, = **Pleonotoma jasminifolia** (Kunth) Miers
Bignonia kerere Aubl., = **Pachyptera kerere** (Aubl.) Sandwith
Bignonia labiatus Cham., = **Tynanthus labiatus** (Cham.) Miers
Bignonia lactiflora Vahl, = **Amphilophium lactiflorum** (Vahl) L. G. Lohmann
Bignonia latifolia Rich.**, = **Callichlamys latifolia** (Rich.) K. Schum.
Bignonia lenta Mart. ex DC., = **Tanaecium pyramidatum** (Rich.) L. G. Lohmann
Bignonia leucopogon Cham., = **Fridericia leucopogon** (Cham.) L. G. Lohmann
Bignonia lilacina (A. H. Gentry) L. G. Lohmann
Bignonia longa Vell.**, = **Lundia longa** (Vell.) DC.
Bignonia longiflora Cav.**
Bignonia magnifica W. Bull
Bignonia magnoliifolia Kunth., = **Amphilophium magnoliifolium** (Kunth) L. G. Lohmann
Bignonia mansoana DC., = **Amphilophium mansoanum** (DC.) L. G. Lohmann
Bignonia marginata Cham., = **Adenocalymma marginatum** (Cham.) DC.
Bignonia melioides S. Moore, = **Pleonotoma melioides** (S. Moore) A. H. Gentry
Bignonia microcalyx G. Mey.
Bignonia mollis Vahl, = **Fridericia mollis** (Vahl) L. G. Lohmann
Bignonia mollissima Kunth, = **Fridericia mollissima** (Kunth) L. G. Lohmann
Bignonia moringifolia DC., = **Adenocalymma moringifolium** (DC.) L. G. Lohmann
Bignonia myriantha Cham., = **Xylophragma myrianthum** (Cham.) Sprague
Bignonia neoheterophylla L. G. Lohmann
Bignonia neouliginosa L. G. Lohmann
Bignonia nocturna (Barb. Rodr.) L. G. Lohmann
Bignonia nodosa Silva Manso, = **Adenocalymma nodosum** (Silva Manso) L. G. Lohmann
Bignonia obovata (Kunth) Spreng., = **Martinella obovata** (Kunth) Bureau & K. Schum.
Bignonia orbiculata Jacq., = **Anemopaegma orbiculatum** (Jacq.) DC.
Bignonia paniculata L., = **Amphilophium paniculatum** (L.) Kunth
Bignonia pannosa DC., = **Amphilophium pannosum** (DC.) Bureau & K. Schum.
Bignonia parkeri DC., = **Amphilophium parkeri** (DC.) L. G. Lohmann
Bignonia patellifera Schltdl., = **Fridericia patellifera** (Schltdl.) L. G. Lohmann
Bignonia pearcei Rusby, = **Fridericia pearcei** (Rusby) L. G. Lohmann
Bignonia pedunculata Vell.**, = **Adenocalymma pedunculatum** (Vell.) L. G. Lohmann
Bignonia perforata Cham., = **Stizophyllum perforatum** (Cham.) Miers
Bignonia perianthomega Vell.**, = **Perianthomega vellozoi** Bureau
Bignonia phellosperma (Hemsl.) L. G. Lohmann
Bignonia pilulifera Rich., = **Fridericia pilulifera** (Rich.) L. G. Lohmann
Bignonia platyphylla Cham., = **Fridericia platyphylla** (Cham.) L. G. Lohmann
Bignonia potosina (K. Schum. & Loes.) L. G. Lohmann
Bignonia prieurii DC.
Bignonia pterocalyx (Sprague ex Urb.) L. G. Lohmann
Bignonia pubescens L., = **Fridericia pubescens** (L.) L. G. Lohmann
Bignonia pulchella Cham., = **Cuspideria pulchella** (Cham.) K. Schum.

Bignonia pulchra Cham., = **Cuspidaria pulchra** (Cham.) L. G. Lohmann
Bignonia pyramidata Rich., = **Tanaecium pyramidatum** (Rich.) L. G. Lohmann
Bignonia quadrivalvis Jacq.**, = **Dolichandra quadrivalvis** (Jacq.) L. G. Lohmann
Bignonia ramentacea (Mart. ex DC.) L. G. Lohmann
Bignonia rego Vell.**, = **Fridericia rego** (Vell.) L. G. Lohmann
Bignonia riparia Kunth, = **Stizophyllum riparium** (Kunth) Sandwith
Bignonia rugosa Schltdl., = **Anemopaegma rugosum** (Schltdl.) Sprague
Bignonia salicifolia Kunth., = **Anemopaegma salicifolium** (Kunth) Sandwith
Bignonia samydoides Cham., = **Fridericia samydoides** (Cham.) L. G. Lohmann
Bignonia scandens Vell.**, = **Anemopaegma chamberlaynii** (Sims) Bureau & K. Schum.
Bignonia sceptrum Cham., = **Cuspidaria sceptrum** (Cham.) L. G. Lohmann
Bignonia sciuripabulum (K. Schum.) L. G. Lohmann
Bignonia sego Vell., = **Fridericia rego** (Vell.) L. G. Lohmann
Bignonia selloi Spreng.**, = **Tanaecium selloi** (Spreng.) L. G. Lohmann
Bignonia sordida (Bureau & K. Schum.) L. G. Lohmann
Bignonia staminea Lam., = **Amphilophium stamineum** (Lam.) L. G. Lohmann
Bignonia ternata Vell.**, = **Adenocalymma ternatum** (Vell.) Corr. Méllo ex Bureau & K. Schum.
Bignonia tetragonoloba Jacq.**, = **Tanaecium tetragonolobum** (Jacq.) L. G. Lohmann
Bignonia tetraquetra Cham., = **Pleonotoma tetraquetra** (Cham.) Bureau
Bignonia trichoclada DC., = **Adenocalymma trichocladum** (DC.) L. G. Lohmann
Bignonia trifoliata Vell., = **Adenocalymma trifoliatum** (Vell.) R. C. Laroche
Bignonia triplinervia Mart. ex DC., = **Fridericia triplinervia** (Mart. ex DC.) L. G. Lohmann
Bignonia uleana (Kraenzl.) L. G. Lohmann
Bignonia uliginosa Gomes, = *Tabebuia cassinoides* (Lam.) DC.
Bignonia uncata Andrews, = **Dolichandra uncata** (Andrews) L. G. Lohmann
Bignonia unguiculata Vell.**, = **Dolichandra unguiculata** (Vell.) L. G. Lohmann
Bignonia unguis-cati L., = **Dolichandra unguis-cati** (L.) L. G. Lohmann
Bignonia variabilis Jacq., = **Pleonotoma variabilis** (Jacq.) Miers
Bignonia venusta Ker Gawl., = **Pyrostegia venusta** (Ker Gawl.) Miers
Bignonia verrucifera Schltdl., = **Mansoa verrucifera** (Schltdl.) A. H. Gentry
Blepharitheca Pichon, = **Cuspidaria** DC.
Blepharitheca argentea (Wawra) Pichon, = **Cuspidaria argentea** (Wawra) Sandwith
Blepharitheca floribunda (DC.) Pichon, = **Cuspidaria floribunda** (DC.) A. H. Gentry
Blepharitheca puberula (Mart. ex DC.) Pichon, = **Cuspidaria puberula** Mart. ex DC.
Bothriopodium Rizzini, = **Amphilophium** Kunth
Bothiopodium glaziovii (Bureau ex K. Schum.) Rizzini, = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Callichlamys Miq.
Callichlamys latifolia (Rich.) K. Schum.
Callichlamys riparia Miq., = **Callichlamys latifolia** (Rich.) K. Schum.
Ceratophytum Pittier, = **Tanaecium** Sw.
Ceratophytum capricorne Pittier, = **Tanaecium tetragonolobum** (Jacq.) L. G. Lohmann
Ceratophytum tetragonolobum (Jacq.) Sprague & Sandwith, = **Tanaecium tetragonolobum** (Jacq.) L. G. Lohmann
Chasmia Schott ex Spreng., = **Fridericia** Mart.
Chasmia Schott ex Kuntze, = **Fridericia** Mart.
Chasmia rego (Vell.) Kuntze, = **Fridericia rego** (Vell.) L. G. Lohmann
Chodanthus Hassl., = **Mansoa** DC.
Chodanthus montecillense Ant. Molina, = **Mansoa montecillensis** (Ant. Molina) C. Nelson
Chodanthus puberulus Seibert, = **Anemopaegma puberulum** (Seibert) Miranda
Chodanthus splendens (Bureau & K. Schum.) Hassl., = **Mansoa difficilis** (Cham.) Bureau & K. Schum.
Clytostoma Miers ex Bureau, = **Bignonia** L.
Clytostoma binatum (Thunb.) Sandwith, = **Bignonia binata** Thunb.
Clytostoma callistegioides (Cham.) Bureau ex Griseb., = **Bignonia callistegioides** Cham.
Clytostoma campanulatum (Cham.) Bureau & K. Schum., = **Bignonia campanulata** Cham.
Clytostoma convolvuloides Bureau & K. Schum.**, = **Bignonia convolvuloides** (Bureau & K. Schum.) L. G. Lohmann
Clytostoma costatum Bureau & K. Schum.**, = **Bignonia costata** (Bureau & K. Schum.) L. G. Lohmann
Clytostoma cuneatum Dugand, = **Bignonia cuneata** (Dugand) L. G. Lohmann
Clytostoma decorum (S. Moore) Bureau & K. Schum., = **Bignonia decora** (S. Moore) L. G. Lohmann
Clytostoma pterocalyx Sprague ex Urb.**, = **Bignonia pterocalyx** (Sprague ex Urb.) L. G. Lohmann
Clytostoma ramentaceum (Mart. ex DC.) Bureau & K. Schum., = **Bignonia ramentacea** (Mart. ex DC.) L. G. Lohmann
Clytostoma sciuripabulum (K. Schum.) Bureau & K. Schum., = **Bignonia sciuripabulum** (K. Schum.) L. G. Lohmann
Clytostoma uleanum Kraenzl., = **Bignonia uleana** (Kraenzl.) L. G. Lohmann
Clytostomanthus Pichon, = **Bignonia** L.
Clytostomanthus decorus (S. Moore) Pichon, = **Bignonia decora** (S. Moore) L. G. Lohmann
Craterotecoma Mart. ex Meisn., = **Lundia** DC.
Craterotecoma parviflora DC., = **Lundia erionema** DC.
Cremastus Miers, = **Cuspidaria** DC.
Cremastus glutinosus (DC.) Miers, = **Cuspidaria sceptrum** (Cham.) L. G. Lohmann
Cremastus lachnaeus Bureau**, = **Cuspidaria lachnaea** (Bureau) L. G. Lohmann
Cremastus pulcher (Cham.) Bureau, = **Cuspidaria pulchra** (Cham.) L. G. Lohmann
Cremastus sceptrum (Cham.) Bureau & K. Schum., = **Cuspidaria sceptrum** (Cham.) L. G. Lohmann
Cupulissa Raf., = **Anemopaegma** Mart. ex Meisn.
Cupulissa grandifolia (Jacq.) Raf., = **Anemopaegma grandifolium** (Jacq.) Merr. & Sandwith
Cuspidaria DC.
Cuspidaria angustidens DC., = **Mansoa angustidens** (DC.) Bureau & K. Schum.
Cuspidaria argentea (Wawra) Sandwith
Cuspidaria bracteata (Bureau & K. Schum.) L. G. Lohmann
Cuspidaria callistegioides (Cham.) DC., = **Bignonia callistegioides** Cham.

Cuspidaria campanulata (Cham.) DC., = **Bignonia campanulata** Cham.
Cuspidaria cinerea (Bureau ex K. Schum.) L. G. Lohmann
Cuspidaria convoluta (Vell.) A. H. Gentry
Cuspidaria corymbifera (Vahl) Baill. ex K. Schum., = **Lundia corymbifera** (Vahl) Sandwith
Cuspidaria cratensis (J. C. Gomes) A. H. Gentry ex L. G. Lohmann
Cuspidaria emmonsii A. H. Gentry
Cuspidaria erubescens (DC.) Bureau, = **Fridericia erubescens** (DC.) L. G. Lohmann
Cuspidaria fasciculata (Vell.) Sond., = **Tynanthus fasciculatus** (Vell.) Miers
Cuspidaria floribunda (DC.) A. H. Gentry
Cuspidaria hymenaea (DC.) M. R. Almeida, = **Mansoa hymenaea** (DC.) A. H. Gentry
Cuspidaria inaequalis (DC. ex Splitg.) L. G. Lohmann
Cuspidaria lachnaea (Bureau) L. G. Lohmann
Cuspidaria lasiantha (Bureau & K. Schum.) L. G. Lohmann
Cuspidaria lateriflora (Mart.) DC.
Cuspidaria multiflora DC.**
Cuspidaria octoptera A. H. Gentry
Cuspidaria pterocarpa (Cham.) DC., = **Cuspidaria convoluta** (Vell.) A. H. Gentry
Cuspidaria puberula Mart. ex DC., = **Cuspidaria simplicifolia** DC.
Cuspidaria pulchella (Cham.) K. Schum.
Cuspidaria pulchra (Cham.) L. G. Lohmann
Cuspidaria ramentacea Mart. ex DC., = **Bignonia ramentacea** (Mart. ex DC.) L. G. Lohmann
Cuspidaria sceptrum (Cham.) L. G. Lohmann
Cuspidaria schumanniana Kuntze, = **Tynanthus schumannianus** (Kuntze) A. H. Gentry
Cuspidaria simplicifolia DC.
Cuspidaria subincana A. H. Gentry
Cuspidaria weberbaueri (Sprague) A. H. Gentry
Cydista Miers, = **Bignonia** L.
Cydista aequinoctialis (L.) Miers, = **Bignonia aequinoctialis** L.
Cydista bracteomana K. Schum., = **Bignonia bracteomana** (K. Schum.) L. G. Lohmann
Cydista decora (S. Moore) A. H. Gentry, = **Bignonia decora** (S. Moore) L. G. Lohmann
Cydista difficilis (Cham.) Miers, = **Mansoa difficilis** (Cham.) Bureau & K. Schum.
Cydista diversifolia (Kunth) Miers, = **Bignonia diversifolia** Kunth
Cydista heterophylla Seibert, = **Bignonia neoheterophylla** L. G. Lohmann
Cydista lilacina A. H. Gentry, = **Bignonia lilacina** (A. H. Gentry) L. G. Lohmann
Cydista potosina (K. Schum. & Loes.) Loes., = **Bignonia potosina** (K. Schum. & Loes.) L. G. Lohmann
Danielia Corr. Méllo ex Verlot, = **Mansoa** DC.
Danielia splendens Corr. Méllo ex Verlot, = **Mansoa difficilis** (Cham.) Bureau & K. Schum.
[*Delostoma* D. Don, Bignoniaceae, Tribe Tecomeae]
Delostoma latifolium (Rich.) Splitg., = **Callichlamys latifolia** (Rich.) K. Schum.
Distictella Kuntze, = **Amphilophium** Kunth
Distictella arenaria A. H. Gentry, = **Amphilophium arenarium** (A. H. Gentry) L. G. Lohmann
Distictella campinae A. Samp., = **Amphilophium campinae** (A. Samp.) L. G. Lohmann
Distictella chocoensis A. H. Gentry, = **Amphilophium chocoense** (A. H. Gentry) L. G. Lohmann
Distictella crassa (Bureau & K. Schum.) Urb., = **Fridericia crassa** (Bureau & K. Schum.) L. G. Lohmann
Distictella cremersii A. H. Gentry, = **Amphilophium cremersii** (A. H. Gentry) L. G. Lohmann
Distictella cuneifolia (DC.) Sandwith, = **Amphilophium cuneifolium** (DC.) L. G. Lohmann
Distictella dasytricha Sandwith, = **Amphilophium dasytrichum** (Sandwith) L. G. Lohmann
Distictella elongata (Vahl) Urb., = **Amphilophium elongatum** (Vahl) L. G. Lohmann
Distictella granulosa (Bureau & K. Schum.) Sandwith, = **Amphilophium granulosum** (Bureau & K. Schum.) L. G. Lohmann
Distictella laevis (Sandwith) A. H. Gentry, = **Amphilophium laeve** (Sandwith) L. G. Lohmann
Distictella lohmanniae A. Pool, = **Amphilophium lohmanniae** (A. Pool) L. G. Lohmann
Distictella magnoliifolia (Kunth) Sandwith, = **Amphilophium magnoliifolium** (Kunth) L. G. Lohmann
Distictella mansoana (DC.) Urb., = **Amphilophium mansoanum** (DC.) L. G. Lohmann
Distictella monophylla Sandwith, = **Amphilophium monophyllum** (Sandwith) L. G. Lohmann
Distictella monophylla var. *laevis* Sandwith, = **Amphilophium laeve** (Sandwith) L. G. Lohmann
Distictella obovata Sandwith, = **Amphilophium obovatum** (Sandwith) L. G. Lohmann
Distictella parkeri (DC.) Sprague & Sandwith, = **Amphilophium parkeri** (DC.) L. G. Lohmann
Distictella pauciflora A. H. Gentry, = **Amphilophium pauciflorum** (A. H. Gentry) L. G. Lohmann
Distictella porphyrotricha Sandwith, = **Amphilophium porphyrotrichum** (Sandwith) L. G. Lohmann
Distictella pulverulenta Sandwith, = **Amphilophium pulverulentum** (Sandwith) L. G. Lohmann
Distictella racemosa (Bureau & K. Schum.) Urb., = **Amphilophium racemosum** (Bureau & K. Schum.) L. G. Lohmann
Distictella reticulata A. H. Gentry, = **Amphilophium reticulatum** (A. H. Gentry) L. G. Lohmann
Distictis Mart. ex Meisn., = **Amphilophium** Kunth
Distictis arthrerion (Mart.) DC., = **Fridericia arthrerion** (Mart.) L. G. Lohmann
Distictis buccinatoria (DC.) A. H. Gentry, = **Amphilophium buccinatorium** (DC.) L. G. Lohmann
Distictis crassa Bureau & K. Schum.**, = **Fridericia crassa** (Bureau & K. Schum.) L. G. Lohmann
Distictis elongata (Vahl) Bureau ex Benth., = **Amphilophium elongatum** (Vahl) L. G. Lohmann
Distictis frutescens (DC.) A. Pool, = **Amphilophium frutescens** (DC.) L. G. Lohmann
Distictis glaziovii (Bureau ex K. Schum.) Bureau & K. Schum., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Distictis gnaphalantha (A. Rich.) Greenm., = **Amphilophium gnaphalanthum** (A. Rich.) L. G. Lohmann
Distictis gnaphalantha (A. Rich.) Urb., = **Amphilophium gnaphalanthum** (A. Rich.) L. G. Lohmann
Distictis granulosa Bureau & K. Schum., = **Amphilophium granulosum** (Bureau & K. Schum.) L. G. Lohmann
Distictis lactiflora (Vahl) DC., = **Amphilophium lactiflorum** (Vahl) L. G. Lohmann
Distictis laxiflora (DC.) Greenm., = **Amphilophium laxiflorum** (DC.) L. G. Lohmann
Distictis mansoana (DC.) Bureau, = **Amphilophium mansoanum** (DC.) L. G. Lohmann
Distictis occidentalis A. H. Gentry, = **Amphilophium occidentale** (A. H. Gentry) L. G. Lohmann

Distictis pulverulenta (Sandwith) A. H. Gentry, = **Amphilophium pulverulentum** (Sandwith) L. G. Lohmann
Distictis racemosa Bureau & K. Schum., = **Amphilophium racemosum** (Bureau & K. Schum.) L. G. Lohmann
Distictis scabriuscula (Mart. ex DC.) A. H. Gentry, = **Amphilophium scabriusculum** (Mart. ex DC.) L. G. Lohmann
Distictis staminea (Lam.) A. H. Gentry, = **Amphilophium stamineum** (Lam.) L. G. Lohmann
Distictis steyermarkii A. H. Gentry, = **Amphilophium steyermarkii** (A. H. Gentry) L. G. Lohmann
Distictis stipularis (Mart. ex DC.) A. H. Gentry, = **Amphilophium frutescens** (DC.) L. G. Lohmann
Dolichandra Cham.
Dolichandra chodatii (Hassl.) L. G. Lohmann
Dolichandra cynanchoides Cham.
Dolichandra dentata (K. Schum.) L. G. Lohmann
Dolichandra quadrivalvis (Jacq.) L. G. Lohmann
Dolichandra steyermarkii (Sandwith) L. G. Lohmann
Dolichandra uncata (Andrews) L. G. Lohmann
Dolichandra unguiculata (Vell.) L. G. Lohmann
Dolichandra unguis-cati (L.) L. G. Lohmann
Doxantha Miers, = **Dolichandra** Cham.
Doxantha capreolata (L.) Miers, = **Bignonia capreolata** L.
Doxantha elongata (Vahl) Miers, = **Amphilophium elongatum** (Vahl) L. G. Lohmann
Doxantha uncata (Andrews) Miers, = **Dolichandra uncata** (Andrews) L. G. Lohmann
Doxantha unguiculata (Vell.) Miers, = **Dolichandra unguiculata** (Vell.) L. G. Lohmann
Doxantha unguis-cati (L.) Miers, = **Dolichandra unguis-cati** (L.) L. G. Lohmann
Endoloma Raf., = **Amphilophium** Kunth
Endoloma purpurea Raf., = **Amphilophium paniculatum** (L.) Kunth
Exsertanthera Pichon, = **Lundia** DC.
Exsertanthera longa (Vell.) Pichon, = **Lundia longa** (Vell.) DC.
Fridericia Mart.
Fridericia arthrerion (Mart.) L. G. Lohmann
Fridericia bahiensis (Schauer ex DC.) L. G. Lohmann
Fridericia bracteolata (DC.) L. G. Lohmann
Fridericia candicans (Rich.) L. G. Lohmann
Fridericia carichanensis (Kunth) L. G. Lohmann
Fridericia caudigera (S. Moore) L. G. Lohmann
Fridericia celastroides (Bureau ex K. Schum.) L. G. Lohmann
Fridericia chica (Bonpl.) L. G. Lohmann
Fridericia cinerea (Bureau ex K. Schum.) L. G. Lohmann
Fridericia cinnamomea (DC.) L. G. Lohmann
Fridericia claussenii (A. DC.) L. G. Lohmann
Fridericia conjugata (Vell.) L. G. Lohmann
Fridericia corchoroides (Cham.) L. G. Lohmann
Fridericia costaricensis (Kraenzl.) L. G. Lohmann
Fridericia crassa (Bureau & K. Schum.) L. G. Lohmann
Fridericia craterophora (DC.) L. G. Lohmann
Fridericia cuneifolia (DC.) L. G. Lohmann
Fridericia dichotoma (Jacq.) L. G. Lohmann
Fridericia dispar (Bureau ex K. Schum.) L. G. Lohmann
Fridericia egensis (Bureau & K. Schum.) L. G. Lohmann
Fridericia elegans (Vell.) L. G. Lohmann
Fridericia erubescens (DC.) L. G. Lohmann
Fridericia fagoides (Cham.) L. G. Lohmann
Fridericia fanshawei (Sandwith) L. G. Lohmann
Fridericia floribunda (Kunth) L. G. Lohmann
Fridericia florida (DC.) L. G. Lohmann
Fridericia formosa (Bureau) L. G. Lohmann
Fridericia grosourdyana (Baill.) L. G. Lohmann
Fridericia japurensis (DC.) L. G. Lohmann
Fridericia lasiantha (Bureau & K. Schum.) L. G. Lohmann, = **Cuspidaria lasiantha** (Bureau & K. Schum.) L. G. Lohmann
Fridericia lauta (Bureau & K. Schum.) L. G. Lohmann
Fridericia leucopogon (Cham.) L. G. Lohmann
Fridericia limae (A. H. Gentry) L. G. Lohmann
Fridericia mollis (Vahl) L. G. Lohmann
Fridericia mollissima (Kunth) L. G. Lohmann
Fridericia monophylla (A. H. Gentry) L. G. Lohmann
Fridericia mutabilis (Bureau & K. Schum.) L. G. Lohmann, = **Tanaecium mutabile** (Bureau & K. Schum.) L. G. Lohmann
Fridericia nicotianiflora (Kraenzl.) L. G. Lohmann
Fridericia nigrescens (Sandwith) L. G. Lohmann
Fridericia oligantha (Bureau & K. Schum.) L. G. Lohmann
Fridericia ornithophila (A. H. Gentry) L. G. Lohmann
Fridericia oxycarpa (Urb.) L. G. Lohmann
Fridericia paradoxa (Sandwith) L. G. Lohmann
Fridericia parviflora (Mart. ex DC.) L. G. Lohmann
Fridericia patellifera (Schltdl.) L. G. Lohmann
Fridericia pearcei (Rusby) L. G. Lohmann
Fridericia platyphylla (Cham.) L. G. Lohmann
Fridericia pliciflora (Mart. ex DC.) L. G. Lohmann
Fridericia podopogon (DC.) L. G. Lohmann
Fridericia poeppigii (DC.) L. G. Lohmann
Fridericia prancei (A. H. Gentry) L. G. Lohmann
Fridericia pubescens (L.) L. G. Lohmann
Fridericia pulchella (Cham.) L. G. Lohmann, = **Cuspidaria pulchella** (Cham.) K. Schum
Fridericia rego (Vell.) L. G. Lohmann
Fridericia samydoides (Cham.) L. G. Lohmann
Fridericia schumanniana (Loes.) L. G. Lohmann
Fridericia simplex (A. H. Gentry) L. G. Lohmann
Fridericia speciosa Mart.**
Fridericia spicata (Bureau & K. Schum.) L. G. Lohmann
Fridericia subexserta (Bureau & K. Schum.) L. G. Lohmann
Fridericia subincana (Mart.) L. G. Lohmann
Fridericia subverticillata (Bureau & K. Schum.) L. G. Lohmann
Fridericia trachyphylla (Bureau & K. Schum.) L. G. Lohmann
Fridericia trailii (Sprague) L. G. Lohmann
Fridericia triplinervia (Mart. ex DC.) L. G. Lohmann
Fridericia truncata (Sprague) L. G. Lohmann
Fridericia tuberculata (DC.) L. G. Lohmann
Fridericia tynanthoides (A. H. Gentry) L. G. Lohmann
Fridericia viscida (Donn. Sm.) L. G. Lohmann
Fridericia whitei (Rusby) L. G. Lohmann
Gardnerodoxa Sandwith, = **Neojobertia** Baill.
Gardnerodoxa mirabilis Sandwith, = **Neojobertia mirabilis** (Sandwith) L. G. Lohmann
Glaziova Bureau, = **Amphilophium** Kunth
Glaziova bauhinioides Bureau ex Baill.**, = **Amphilophium bauhinioides** (Bureau ex Baill.) L. G. Lohmann
Hanburyophyton Bureau, = **Mansoa** DC.
Hanburyophyton xanthinum Bureau, = **Mansoa lanceolata** (DC.) A. H. Gentry
Haplolophium Cham., = **Amphilophium** Kunth
Haplolophium blanchetii DC., = **Amphilophium blanchetii** (DC.) Bureau & K. Schum.
Haplolophium bracteatum Cham., = **Amphilophium bracteatum** (Cham.) L. G. Lohmann
Haplolophium dusenianum Kraenzl., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Haplolophium glaziovii (Bureau ex K. Schum.) A. H. Gentry, = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann

Haplolophium nunezii A. H. Gentry, = **Amphilophium nunezii** (A. H. Gentry) L. G. Lohmann
Haplolophium rodriguesii A. H. Gentry, = **Amphilophium rodriguesii** (A. H. Gentry) L. G. Lohmann
Heterocalycium Rauschert, = **Xylophragma** Sprague
Heterocalycium heterocalyx (Bureau & K. Schum.) Rauschert, = **Xylophragma heterocalyx** (Bureau & K. Schum.) A. H. Gentry
Hilariophyton Pichon, = **Tanaecium** Sw.
Hilariophyton brasiliensis (Baill.) Pichon, = **Tanaecium neobrasiliense** L. G. Lohmann
[*Jacaranda* Juss., Bignoniaeceae, Tribe Jacarandeae]
Jacaranda alba (Aubl.) Spreng., = **Adenocalymma album** (Aubl.) L. G. Lohmann
Jacaranda arvensis (Vell.) Steud., = **Anemopaegma arvense** (Vell.) Stellfeld ex J. F. Souza
Jacaranda orbiculata (Jacq.) Spreng., = **Anemopaegma orbiculatum** (Jacq.) DC.
Kuhlmannia J. C. Gomes, = **Pleonotoma** Miers
Kuhlmannia colatinensis J. C. Gomes, = **Pleonotoma albiflora** (Salzm. ex DC.) A. H. Gentry
Leucocalantha Barb. Rodr., = **Pachyptera** DC. ex Meisn.
Leucocalantha aromatica Barb. Rodr., = **Pachyptera aromatica** (Barb. Rodr.) L. G. Lohmann
Leucocolanthe, orth. var., = **Pachyptera** DC. ex Meisn.
Levya Bureau ex Baill., = **Bignonia** L.
Levya nicaraguensis Bureau ex Baill., = **Bignonia aequinoctialis** L.
Lundia DC.
Lundia chica (Bonpl.) Seem., = **Fridericia chica** (Bonpl.) L. G. Lohmann
Lundia cordata (Vell.) DC., = **Lundia corymbifera** (Vahl) Sandwith
Lundia corymbifera (Vahl) Sandwith
Lundia damazii, orth. var., = **Lundia damazioi** C. DC.
Lundia damazioi C. DC.
Lundia densiflora DC.**
Lundia erionema DC.
Lundia gardneri Sandwith
Lundia glabra DC., = **Lundia nitidula** DC.
Lundia heliocalyx A. H. Gentry
Lundia laevis Kaehler
Lundia longa (Vell.) DC.
Lundia neolonga L. G. Lohmann, = **Lundia damazioi** C. DC.
Lundia nitidula DC.
Lundia nitidula var. *virginalis* (DC.) Bureau, = **Lundia virginalis** DC.
Lundia obliqua Sond.**
Lundia puberula Pittier
Lundia spruceana Bureau
Lundia virginalis DC.**
Lundia virginalis var. *nitidula* (DC.) A. H. Gentry, = **Lundia nitidula** DC.
Macfadyena A. DC., = **Dolichandra** Cham.
Macfadyena bipinnata S. Moore, = **Adenocalymma bipinnatum** (S. Moore) L. G. Lohmann
Macfadyena bracteosa (DC.) Benth., = **Adenocalymma bracteosa** (DC.) L. G. Lohmann
Macfadyena corymbosa (Vent.) Griseb., = **Bignonia corymbosa** (Vent.) L. G. Lohmann
Macfadyena cynanchoides (Cham.) Morong, = **Dolichandra cynanchoides** Cham.
Macfadyena dentata K. Schum.**, = **Dolichandra dentata** (K. Schum.) L. G. Lohmann
Macfadyena fallax (Cham.) S. Moore, = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Macfadyena japurensis (DC.) Miers, = **Fridericia japurensis** (DC.) L. G. Lohmann
Macfadyena obovata (Kunth) Miers, = **Martinella obovata** (Kunth) Bureau & K. Schum.
Macfadyena phellosperma Hemsl., = **Bignonia phellosperma** (Hemsl.) L. G. Lohmann
Macfadyena podopogon (DC.) Griseb., = **Fridericia podopogon** (DC.) L. G. Lohmann
Macfadyena uncata (Andrew) Sprague & Sandwith, = **Dolichandra uncata** (Andrews) L. G. Lohmann
Macfadyena uncinata (G. Mey.) A. DC., = **Dolichandra uncata** (Andrews) L. G. Lohmann
Macfadyena unguis-cati (L.) A. H. Gentry, = **Dolichandra unguis-cati** (L.) L. G. Lohmann
Macranthisiphon Bureau ex K. Schum., = **Bignonia** L.
Macranthisiphon longiflorus (Cav.) K. Schum., = **Bignonia longiflora** Cav.
Macrodiscus Bureau, = **Amphilophium** Kunth
Macrodiscus lactiflorus (Vahl) Bureau ex K. Schum., = **Amphilophium lactiflorum** (Vahl) L. G. Lohmann
Macrodiscus rigescens (Jacq.) Bureau, = **Amphilophium lactiflorum** (Vahl) L. G. Lohmann
Manaosella J. C. Gomes
Manaosella cordifolia (DC.) A. H. Gentry
Manaosella erythraea = **Pachyptera erythraea** (Dugand) A. H. Gentry
Manaosella platydactyla (Barb. Rodr.) J. C. Gomes, = **Manaosella cordifolia** (DC.) A. H. Gentry
Mansoa DC.
Mansoa alliacea (Lam.) A. H. Gentry
Mansoa angustidens (DC.) Bureau & K. Schum.
Mansoa difficilis (Cham.) Bureau & K. Schum.
Mansoa erythraea (Dugand) A. H. Gentry, = **Pachyptera erythraea** (Dugand) A. H. Gentry
Mansoa glaziovii Bureau & K. Schum.**
Mansoa hirsuta DC.
Mansoa hymenaea (DC.) A. H. Gentry
Mansoa kerere (Aubl.) A. H. Gentry, = **Pachyptera kerere** (Aubl.) Sandwith
Mansoa lanceolata (DC.) A. H. Gentry
Mansoa montecillensis (Ant. Molina) C. Nelson
Mansoa onohualcoides A. H. Gentry
Mansoa parvifolia (A. H. Gentry) A. H. Gentry
Mansoa standleyi (Steyerm.) A. H. Gentry
Mansoa truncata Sprague, = **Fridericia truncata** (Sprague) L. G. Lohmann
Mansoa ventricosa A. H. Gentry, = **Pachyptera ventricosa** (A. H. Gentry) L. G. Lohmann
Mansoa verrucifera (Schltdl.) A. H. Gentry
Martinella Baill.
Martinella iquitoensis A. Samp.
Martinella martinii (DC.) Baill. ex K. Schum., = **Martinella obovata** (Kunth) Bureau & K. Schum.
Martinella obovata (Kunth) Bureau & K. Schum.
Martinella verrucosa (Standl.) Standl., = **Fridericia schumanniana** (Loes.) L. G. Lohmann
Melloa Bureau, = **Dolichandra** Cham.
Melloa populifolia (DC.) Bureau, = **Dolichandra quadrivalvis** (Jacq.) L. G. Lohmann
Melloa quadrivalis (Jacq.) A. H. Gentry, = **Dolichandra quadrivalvis** (Jacq.) L. G. Lohmann
Memora Miers, = **Adenocalymma** Mart. ex Meisn.
Memora adenophora Sandwith, = **Adenocalymma adnophorum** (Sandwith) L. G. Lohmann
Memora alba (Aubl.) Miers, = **Adenocalymma album** (Aubl.) L. G. Lohmann

Memora albiflora (Salzm. ex DC.) Miers, = **Pleonotoma albiflora** (Salzm. ex DC.) A. H. Gentry
Memora allamandiflora Bureau ex K. Schum., = **Adenocalymma allamandiflorum** (Bureau ex K. Schum.) L. G. Lohmann
Memora aspericarpa A. H. Gentry, = **Adenocalymma aspericarpum** (A. H. Gentry) L. G. Lohmann
Memora axillaris K. Schum.**, = **Adenocalymma axillare** (K. Schum.) L. G. Lohmann
Memora bilabiata Sprague, = **Tanaecium bilabiatum** (Sprague) L. G. Lohmann
Memora bipinnata (S. Moore) A. H. Gentry, = **Adenocalymma bipinnatum** (S. Moore) L. G. Lohmann
Memora biternata A. Samp., = **Adenocalymma biternatum** (A. Samp.) L. G. Lohmann
Memora bracteosa (DC.) Bureau ex K. Schum., = **Adenocalymma bracteosum** (DC.) L. G. Lohmann
Memora campicola Pilg.**, = **Adenocalymma campicola** (Pilg.) L. G. Lohmann
Memora candolleana (Mart. ex DC.) Miers, = **Neojobertia candolleana** (Mart. ex DC.) Bureau & K. Schum.
Memora cidii A. H. Gentry ex Hauk, = **Adenocalymma cidii** (A. H. Gentry ex Hauk) L. G. Lohmann
Memora cladotricha Sandwith, = **Adenocalymma cladotricum** (Sandwith) L. G. Lohmann
Memora contracta A. H. Gentry ex Hauk, = **Adenocalymma contractum** (A. H. Gentry ex Hauk) L. G. Lohmann
Memora cristacalyx A. H. Gentry, = **Adenocalymma cristacalyx** (A. H. Gentry) L. G. Lohmann
Memora croatii A. H. Gentry, = **Adenocalymma croatii** (A. H. Gentry) L. G. Lohmann
Memora fallax (Cham.) Bureau, = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Memora flavida (DC.) Bureau & K. Schum., = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Memora flaviflora (Miq.) Pulle, = **Adenocalymma flaviflorum** (Miq.) L. G. Lohmann
Memora fluminensis (Vell.) Miers, = **Pleonotoma fluminensis** (Vell.) A. H. Gentry
Memora heterophylla (Kraenzl.) Sandwith, = **Adenocalymma heterophyllum** Kraenzl.
Memora imperatoris-maximilianii (Wawra) A. H. Gentry, = **Adenocalymma imperatoris-maximilianii** (Wawra) L. G. Lohmann
Memora involucrata Bureau & K. Schum., = **Adenocalymma involucratum** (Bureau & K. Schum.) L. G. Lohmann
Memora juliae A. H. Gentry, = **Adenocalymma juliae** (A. H. Gentry) L. G. Lohmann
Memora longilinea A. Samp., = **Adenocalymma longilineum** (A. Samp.) L. G. Lohmann
Memora magnifica (Mart. ex DC.) Bureau, = **Adenocalymma magnificum** Mart. ex DC.
Memora mollis A. H. Gentry, = **Adenocalymma molle** (A. H. Gentry) L. G. Lohmann
Memora moringifolia (DC.) Sandwith, = **Adenocalymma moringifolium** (DC.) L. G. Lohmann
Memora nodosa (Silva Manso) Miers, = **Adenocalymma nodosum** (Silva Manso) L. G. Lohmann
Memora patula Miers, = **Adenocalymma patulum** (Miers) L. G. Lohmann
Memora paucifoliolata A. H. Gentry, = **Adenocalymma paucifoliolatum** (A. H. Gentry) L. G. Lohmann
Memora pedunculata (Vell.) Miers, = **Adenocalymma pedunculatum** (Vell.) L. G. Lohmann
Memora peregrina (Miers) Sandwith, = **Adenocalymma peregrinum** (Miers) L. G. Lohmann
Memora perianthomega (Bell.) Miers, = **Perianthomega vellozoi** Bureau
Memora pseudopatula A. H. Gentry, = **Adenocalymma peregrinum** (A. H. Gentry) L. G. Lohmann
Memora pubescens (Spreng.) K. Schum., = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Memora racemosa A. H. Gentry, = **Adenocalymma racemosum** (A. H. Gentry) L. G. Lohmann
Memora sastrei A. H. Gentry, = **Adenocalymma sastrei** (A. H. Gentry ex Hauk) L. G. Lohmann
Memora schomburgkii (DC.) Miers, = **Adenocalymma schomburgkii** (DC.) L. G. Lohmann
Memora tanaeciicarpa A. H. Gentry, = **Adenocalymma tanaeciicarpum** (A. H. Gentry) L. G. Lohmann
Memora tetraquetra (Cham.) Miers, = **Pleonotoma tetraquetra** (Cham.) Bureau
Memora valida K. Schum., = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Memora velutina A. H. Gentry ex Hauk, = **Adenocalymma velutinum** (A. H. Gentry) L. G. Lohmann
Microbignonia Kraenzl., = **Dolichandra** Cham.
Microbignonia auristellae Kraenzl., = **Dolichandra unguiscati** (L.) L. G. Lohmann
Micropaegma Pichon, = **Bignonia** L.
Micropaegma brachycalyx (Bureau & K. Schum.) Pichon, = **Bignonia prieurii** DC.
Mussatia Bureau ex Baill., = **Bignonia** L.
Mussatia caudiculata (Standl.) Seibert, = **Tanaecium caudiculatum** (Standl.) L. G. Lohmann
Mussatia hyacinthina (Standl.) Sandwith, = **Bignonia hyancinthina** (Standl.) L. G. Lohmann
Mussatia prieurii (DC.) Bureau ex K. Schum., = **Bignonia prieurii** DC.
Neojobertia Baill.
Neojobertia brasiliensis Baill., = **Neojobertia candolleana** (Mart. ex DC.) Bureau & K. Schum.
Neojobertia candolleana (Mart. ex DC.) Bureau & K. Schum.
Neojobertia mirabilis (Sandwith) L. G. Lohmann
Neomacfadya Baill., = **Fridericia** Mart.
Neomacfadya podopogon (DC.) Baill. ex K. Schum., = **Fridericia podopogon** (DC.) L. G. Lohmann
Neomacfadyena, orth. var., = **Fridericia** Mart.
Nestoria Urb., = **Pleonotoma** Miers
Nestoria albiflora (Salzm. ex DC.) Sandwith, = **Pleonotoma albiflora** (Salzm. ex DC.) A. H. Gentry
Nestoria obtusifoliolata (Bureau & K. Schum.) Urb., = **Pleonotoma albiflora** (Salzm. ex DC.) A. H. Gentry
Neves-armondia K. Schum., = **Amphilophium** Kunth
Neves-armondia cordifolia (Mart.) K. Schum., = **Amphilophium falcatum** (Vell.) L. G. Lohmann
Nouletia Endl., = **Cuspidaria** DC.
Nouletia pterocarpa (Cham.) Pichon, = **Cuspidaria convoluta** (Vell.) A. H. Gentry
Odontotecoma Bureau & K. Schum., = **Adenocalymma** Mart. ex Meisn.
Odontotecoma fulgens Bureau & K. Schum., = **Adenocalymma cymbalum** (Cham.) Bureau & K. Schum.
Onohualcoa Lundell, = **Mansoa** DC.
Onohualcoa seleri (Loes.) Lundell, = **Mansoa verrucifera** (Schltdl.) A. H. Gentry
Onohualcoa verricifera (Schltdl.) A. H. Gentry, = **Mansoa verrucifera** (Schltdl.) A. H. Gentry
Orthotheca Pichon, = **Xylophragma** Sprague
Orthotheca heterocalyx (Bureau & K. Schum.) Pichon, = **Xylophragma heterocalyx** (Bureau & K. Schum.) A. H. Gentry
Osmhydrophora Barb. Rodr., = **Bignonia** L.

Osmhydrophora nocturna Barb. Rodr., = **Bignonia nocturna** (Barb. Rodr.) L. G. Lohmann
Osmohydrophora, orth. var., = **Bignonia** L.
Pachyptera DC. ex Meisn.
Pachyptera alliacea (Lam.) A. H. Gentry, = **Mansoa alliacea** (Lam.) A. H. Gentry
Pachyptera aromatica (Barb. Rodr.) L. G. Lohmann
Pachyptera erythraea (Dugand) A. H. Gentry
Pachyptera foveolata DC., = **Pachyptera kerere** (Aubl.) Sandwith
Pachyptera hymenaea (DC.) A. H. Gentry, = **Mansoa hymenaea** (DC.) A. H. Gentry
Pachyptera kerere (Aubl.) Sandwith
Pachyptera kerere var. *erythraea* Dugand, = **Pachyptera erythraea** (Dugand) A. H. Gentry
Pachyptera parvifolia A. H. Gentry, = **Mansoa parvifolia** (A. H. Gentry) A. H. Gentry
Pachyptera standleyi (Steyerm.) A. H. Gentry, = **Mansoa standleyi** (Steyerm.) A. H. Gentry
Pachyptera ventricosa (A. H. Gentry) L. G. Lohmann
Panterpa Miers, = **Fridericia** Mart.
Panterpa dichotoma (Jacq.) Miers, = **Fridericia dichotoma** (Jacq.) L. G. Lohmann
Panterpa leucopogon (Cham.) Miers, = **Fridericia leucopogon** (Cham.) L. G. Lohmann
Panterpa mollissima (Kunth) Miers, = **Fridericia mollissima** (Kunth) L. G. Lohmann
Panterpa prieurii (DC.) Miers, = **Bignonia prieurii** DC.
Panterpa puberula (Mart. ex DC.) Miers, = **Cuspidaria puberula** Mart. ex DC.
Parabignonia Bureau ex K. Schum., = **Dolichandra** Cham.
Parabignonia chodatii (Hassl.) A. H. Gentry, = **Dolichandra chodatii** (Hassl.) L. G. Lohmann
Parabignonia maximillianii (Mart. ex DC.) Bureau ex K. Schum., = **Dolichandra unguiculata** (Vell.) L. G. Lohmann
Parabignonia steyermarkii Sandwith, = **Dolichandra steyermarkii** (Sandwith) L. G. Lohmann
Parabignonia unguiculata (Vell.) A. H. Gentry, = **Dolichandra unguiculata** (Vell.) L. G. Lohmann
Paracarpaea Pichon, = **Cuspidaria** DC.
Paracarpaea pulchella (Cham.) Pichon, = **Cuspidaria pulchella** (Cham.) K. Schum.
Paradolichandra Hassl., = **Dolichandra** Cham.
Paradolichandra chodatii Hassl., = **Dolichandra chodatii** (Hassl.) L. G. Lohmann
Paragonia Bureau, = **Tanaecium** Sw.
Paragonia brasiliensis (Baill.) A. H. Gentry, = **Tanaecium neobrasiliense** L. G. Lohmann
Paragonia pyramidata (Rich.) Bureau, = **Tanaecium pyramidatum** (Rich.) L. G. Lohmann
Paragonia schumanniana Loes., = **Fridericia schumanniana** (Loes.) L. G. Lohmann
Paramansoa Baill., = **Fridericia** Mart.
Paramansoa grosourdyana Baill.**, = **Fridericia grosourdyana** (Baill.) L. G. Lohmann
[*Peltospermum* DC., = *Aspidosperma* Mart. & Zucc., Apocynaceae]
Peltospermum orbiculatum (Jacq.) DC. ex Meisn., = **Anemopaegma orbiculatum** (Jacq.) A. DC.
Pentelesia Raf., = **Fridericia** Mart.
Pentelesia discolor Raf., = **Fridericia carichanensis** (Kunth) L. G. Lohmann
Perianthomega Bureau ex Baill.
Perianthomega vellozoi Bureau
Periarrabidaea A. Samp.**, = **Tanaecium** Sw.
Periarrabidaea truncata A. Samp., = **Tanaecium truncatum** (A. Samp.) L. G. Lohmann
Petastoma Miers., = **Fridericia** Mart.
Petastoma caudiculata Standl., = **Tanaecium caudiculatum** (Standl.) L. G. Lohmann
Petastoma claussenii (A. DC.) Miers, = **Fridericia claussenii** (A. DC.) L. G. Lohmann
Petastoma corymbiferum (Vahl) Miers, = **Lundia corymbifera** (Vahl) Sandwith
Petastoma cuneifolium (DC.) Bureau & K. Schum., = **Fridericia cuneifolia** (DC.) L. G. Lohmann
Petastoma formosum Bureau**, = **Fridericia formosa** (Bureau) L. G. Lohmann
Petastoma kerere (Aubl.) Schnee, = **Pachyptera kerere** (Aubl.) Sandwith
Petastoma leucopogon (Cham.) Bureau ex Warm., = **Fridericia leucopogon** (Cham.) L. G. Lohmann
Petastoma paradoxum Sandwith, = **Fridericia paradoxa** (Sandwith) L. G. Lohmann
Petastoma patelliferum (Schltdl.) Miers, = **Fridericia patellifera** (Schltdl.) L. G. Lohmann
Petastoma platyphyllum (DC.) Miers, = **Xylophragma platyphyllum** (DC.) L. G. Lohmann
Petastoma poeppigii (DC.) Sandwith, = **Fridericia poeppigii** (DC.) L. G. Lohmann
Petastoma pubescens (L.) Miers, = **Fridericia pubescens** (L.) L. G. Lohmann
Petastoma samydoides (Cham.) Sandwith, = **Fridericia samydoides** (Cham.) L. G. Lohmann
Petastoma sceptrum (Cham.) Miers, = **Cuspidaria sceptrum** (Cham.) L. G. Lohmann
Petastoma trachyphylla Bureau & K. Schum., = **Fridericia trachyphylla** (Bureau & K. Schum.) L. G. Lohmann
Petastoma triplinervia (Mart. ex DC.) Miers, = **Fridericia triplinervia** (Mart. ex DC.) L. G. Lohmann
Petastoma truncatum (Sprague) Hassl., = **Fridericia truncata** (Sprague) L. G. Lohmann
Petastoma whitei (Rusby) Sandwith, = **Fridericia whitei** (Rusby) L. G. Lohmann
Phaedranthus Miers, = **Amphilophium** Kunth
Phaedranthus buccinatorius (DC.) Miers, = **Amphilophium buccinatorium** (DC.) L. G. Lohmann
Phaedranthus lindleyanus Miers, = **Amphilophium buccinatorium** (DC.) L. G. Lohmann
Pharseophora Miers, = **Adenocalymma** Mart. ex Meisn.
Pharseophora bracteosa (DC.) Miers, = **Adenocalymma bracteosum** (DC.) L. G. Lohmann
Pharseophora fallax (Cham.) Miers, = **Adenocalymma pubescens** (Spreng.) L. G. Lohmann
Phryganocydia Mart. ex Bureau, = **Bignonia** L.
Phryganocydia corymbosa (Vent.) Bureau ex K. Schum., = **Bignonia corymbosa** (Vent.) L. G. Lohmann
Phryganocydia phellosperma (Hemsl.) Sandwith, = **Bignonia phellosperma** (Hemsl.) L. G. Lohmann
Phryganocydia uliginosa Dugand, = **Bignonia neouliginosa** L. G. Lohmann
Phrygiobureaua Kuntze, = **Bignonia** L.
Phrygiobureaua corymbosa (Vent.) Kuntze, = **Bignonia corymbosa** (Vent.) L. G. Lohmann
Piriadicus Pichon, = **Fridericia** Mart.
Piriadacus erubescens (DC.) Pichon, = **Fridericia erubescens** (DC.) L. G. Lohmann
Pithecoctenium Mart. ex DC., = **Amphilophium** Kunth
Pithecoctenium buccinatorium DC., = **Amphilophium buccinatorium** (DC.) L. G. Lohmann
Pithecoctenium buccinatorium var. *subinclusum* DC., = **Amphilophium buccinatorium** (DC.) L. G. Lohmann

Pithecoctenium callistegioides (Cham.) Niederl., = **Bignonia callistegioides** Cham.
Pithecoctenium carolinae (Lindl.) G. Nicholson, = **Amphilophium carolinae** (Lindl.) L. G. Lohmann
Pithecoctenium crucigerum (L.) A. H. Gentry, = **Amphilophium crucigerum** (L.) L. G. Lohmann
Pithecoctenium cuneifolium DC., = **Amphilophium cuneifolium** (DC.) L. G. Lohmann
Pithecoctenium cynanchoides DC., = **Amphilophium carolinae** (Lindl.) L. G. Lohmann
Pithecoctenium dolichoides (Cham.) Bureau ex K. Schum., = **Amphilophium dolichoides** (Cham.) L. G. Lohmann
Pithecoctenium echinatum (Jacq.) Baill., = **Amphilophium crucigerum** (L.) L. G. Lohmann
Pithecoctenium elongatum (Vahl) Klotzch, = **Amphilophium elongatum** (Vahl) L. G. Lohmann
Pithecoctenium falcatum (Vell.) A. Pool, = **Amphilophium falcatum** (Vell.) L. G. Lohmann
Pithecoctenium frutescens DC., = **Amphilophium frutescens** (DC.) L. G. Lohmann
Pithecoctenium glaziovii Bureau ex K. Schum., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Pithecoctenium granulosum Klotzsch, = **Amphilophium granulosum** (Bureau & K. Schum.) L. G. Lohmann
Pithecoctenium granulosum (Bureau & K. Schum.) Sprague & Sandwith, = **Amphilophium granulosum** (Bureau & K. Schum.) L. G. Lohmann
Pithecoctenium laxiflorum DC., = **Amphilophium laxiflorum** (DC.) L. G. Lohmann
Pithecoctenium parviflorum Mart. ex DC.**, = **Fridericia parviflora** (Mart. ex DC.) L. G. Lohmann
Pithecoctenium scabriusculum Mart. ex DC., = **Amphilophium scabriusculum** (Mart. ex DC.) L. G. Lohmann
Pithecoctenium sciuripabulum (K. Schum.) Corr. Méllo, = **Bignonia sciuripabulum** (K. Schum.) L. G. Lohmann
Pithecoctenium stipulare Mart. ex DC., = **Amphilophium frutescens** (DC.) L. G. Lohmann
Platolaria Raf., = **Anemopaegma** Mart. ex Meisn.
Platolaria flavescens Raf., = **Anemopaegma orbiculatum** (Jacq.) A. Gentry
Pleonotoma Miers
Pleonotoma albiflora (Salzm. ex DC.) A. H. Gentry
Pleonotoma bracteata A. H. Gentry
Pleonotoma castelnaei (Bureau) Sandwith
Pleonotoma clematis (Kunth) Miers
Pleonotoma dendrotricha Sandwith
Pleonotoma diversifolium (Kunth) Bureau & K. Schum., = **Bignonia diversifolia** Kunth
Pleonotoma echitidea Sprague & Sandwith
Pleonotoma exserta A. H. Gentry
Pleonotoma fissicalyx B. M. Gomes & Proença
Pleonotoma flavida (DC.) Miers, = **Adenocalymma validum** (K. Schum.) L. G. Lohmann
Pleonotoma fluminensis (Vell.) A. H. Gentry
Pleonotoma imperatoris-maximilianii (Wawra) Bureau & K. Schum., = **Adenocalymma imperatoris-maximilianii** (Wawra) L. G. Lohmann
Pleonotoma inaequalis (DC. ex Splitg.) Miers, = **Cuspidaria inaequalis** (DC. ex Splitg.) L. G. Lohmann
Pleonotoma jasminifolia (Kunth) Miers
Pleonotoma lanceolata (DC.) Miers, = **Mansoa lanceolata** (DC.) A. H. Gentry
Pleonotoma longiflora B. M. Gomes & Proença
Pleonotoma melioides (S. Moore) A. H. Gentry
Pleonotoma moringifolia (DC.) Miers, = **Adenocalymma moringifolium** (DC.) L. G. Lohmann
Pleonotoma orientalis Sandwith
Pleonotoma pavettiflora Sandwith
Pleonotoma peregrina Miers, = **Adenocalymma peregrinum** (Miers) L. G. Lohmann
Pleonotoma stichadenia K. Schum.**
Pleonotoma tetraquetra (Cham.) Bureau
Pleonotoma variabilis (Jacq.) Miers
Pleonotoma variabilis var. *castelnaei* Bureau, = **Pleonotoma castelnaei** (Bureau) Sandwith
Potamoganos Sandwith, = **Bignonia** L.
Potamoganos microcalyx (G. Mey.) Sandwith, = **Bignonia microcalyx** G. Mey.
Pseudocalymma A. Samp. & Kuhlm., = **Mansoa** DC.
Pseudocalymma alliaceum (Lam.) Sandwith, = **Mansoa alliacea** (Lam.) A. H. Gentry
Pseudocalymma elegans (Vell.) Kuhlm., = **Fridericia elegans** (Vell.) L. G. Lohmann
Pseudocalymma hymenaeum (DC.) Sandwith, = **Mansoa hymenaea** (DC.) A. H. Gentry
Pseudocalymma laevigatum (Bureau & K. Schum.) A. Samp. & Kuhlm., = **Mansoa hymenaea** (DC.) A. H. Gentry
Pseudocalymma standleyi Steyerm., = **Mansoa standleyi** (Steyerm.) A. H. Gentry
Pseudocalymna, orth. var., = **Mansoa** DC.
Pseudocatalpa A. H. Gentry, = **Tanaecium** Sw.
Pseudocatalpa caudiculata (Standl.) A. H. Gentry, = **Tanaecium caudiculatum** (Standl.) L. G. Lohmann
Pseudopaegma Urb., = **Anemopaegma** Mart. ex Meisn.
Pseudopaegma colombianum Sandwith**, = **Anemopaegma colombianum** (Sandwith) A. H. Gentry
Pseudopaegma insculptum Sandwith, = **Anemopaegma insculptum** (Sandwith) A. H. Gentry
Pseudopaegma jucundum (Bureau & K. Schu.) Urb., = **Anemopaegma jucundum** Bureau & K. Schum.
Pseudopaegma longidens (Mart. ex DC.) Urb., = **Anemopaegma longidens** Mart. ex DC.
Pseudopaegma mirabile Sandwith, = **Anemopaegma mirabile** (Sandwith) A. H. Gentry
Pseudopaegma oligoneuron Sprague & Sandwith, = **Anemopaegma oligoneuron** (Sprague & Sandwith) A. H. Gentry
Pyrostegia C. Presl
Pyrostegia cinerea Bureau ex K. Schum., = **Cuspidaria cinerea** (Bureau ex K. Schum.) L. G. Lohmann
Pyrostegia dichotoma Miers ex K. Schum., = **Pyrostegia venusta** (Ker Gawl.) Miers
Pyrostegia ignea (Vell.) C. Presl, = **Pyrostegia venusta** (Ker Gawl.) Miers
Pyrostegia lauta Miers, = **Fridericia lauta** (Bureau & K. Schum.) L. G. Lohmann
Pyrostegia longiflora (Cav.) Miers, = **Bignonia longiflora** Cav.
Pyrostegia millingtonioides Sandwith
Pyrostegia venusta (Ker Gawl.) Miers
Roentgenia Urb., = **Bignonia** L.
Roentgenia bracteomana (K. Schum.) Urb., = **Bignonia bracteomana** (K. Schum.) L. G. Lohmann
Roentgoenia sordida (Bureau & K. Schum.) Sprague & Sandwith, = **Bignonia sordida** (Bureau & K. Schum.) L. G. Lohmann
Rojasiophyton Hassl., = **Xylophragma** Sprague
Rojasiophyton tuberculatum Hassl., = **Xylophragma pratense** (Bureau & K. Schum.) Sprague
Saldanhaea Bureau, = **Cuspidaria** DC.
Saldanhaea argentea (Wawra) J. C. Gomes, = **Cuspidaria argentea** (Wawra) Sandwith
Saldanhaea bracteata Bureau & K. Schum., = **Cuspidaria cratensis** (J. C. Gomes) A. H. Gentry ex L. G. Lohmann

Saldanhaea costaricensis Kraenzl.**, = **Fridericia costaricensis** (Kraenzl.) L. G. Lohmann
Saldanhaea cratensis J. C. Gomes, = **Cuspidaria cratensis** (J. C. Gomes) A. H. Gentry ex L. G. Lohmann
Saldanhaea floribunda (DC.) Sandwith, = **Cuspidaria floribunda** (DC.) A. H. Gentry
Saldanhaea heterocalyx Bureau & K. Schum.**, = **Xylophragma heterocalyx** (Bureau & K. Schum.) A. H. Gentry
Saldanhaea lateriflora (Mart.) Bureau, = **Cuspidaria lateriflora** (Mart.) DC.
Saldanhaea myriantha (Cham.) Bureau, = **Xylophragma myrianthum** (Cham.) Sprague
Saldanhaea pratensis Bureau & K. Schum.**, = **Xylophragma pratense** (Bureau & K. Schum.) Sprague
Saldanhaea puberula (Mart. ex DC.) J. C. Gomes, = **Cuspidaria puberula** Mart. ex DC.
Saldanhaea seemanniana Kuntze, = **Xylophragma seemannianum** (Kuntze) Sprague
Saldanhaea weberbaueri (Sprague) Sandwith, = **Cuspidaria weberbaueri** (Sprague) A. H. Gentry
Sampaiella J. C. Gomes, = **Adenocalymma** Mart. ex Meisn.
Sampaiella trichoclada (DC.) J. C. Gomes, = **Adenocalymma trichocladum** (DC.) L. G. Lohmann
Sanhilaria Baill., = **Tanaecium** Sw.
Sanhilaria brasiliensis Baill., = **Tanaecium neobrasiliense** L. G. Lohmann
Saritaea Dugand, = **Bignonia** L.
Saritaea magnifica (W. Bull) Dugand, = **Bignonia magnifica** W. Bull
Saritaea triplinvervia (Mart. ex DC.) Dugand, = **Fridericia triplinervia** (Mart. ex DC.) L. G. Lohmann
Schizopsis Bureau, = **Tynanthus** Miers
Schizopsis gondotiana, orth. var., = **Tynanthus goudotianus** (Bureau) Miers
Schizopsis goudotiana Bureau, = **Tynanthus goudotianus** (Bureau) Miers
Schizopsis labiata (Cham.) Bureau ex Baill., = **Tynanthus labiatus** (Cham.) Miers
Schizopsis panurensis Bureau, = **Tynanthus panurensis** (Bureau) Sandwith
Schizopsis polyantha Bureau**, = **Tynanthus polyanthus** (Bureau) Sandwith
Scobinaria Siebert, = **Fridericia** Mart.
Scobinaria japurensis (DC.) Sandwith, = **Fridericia japurensis** (DC.) L. G. Lohmann
Scobinaria verrucosa (Standl.) Seibert, = **Fridericia schumanniana** (Loes.) L. G. Lohmann
Sererera Raf., = **Pachyptera** DC. ex Meisn.
Sererera heterophylla Raf., = **Pachyptera kerere** (Aubl.) Sandwith
Setilobus Baill., = **Cuspidaria** DC.
Setilobus bracteatus Baill. ex Bureau & K. Schum.**, = **Cuspidaria bracteata** (Bureau & K. Schum.) L. G. Lohmann
Sideropogon Pichon, = **Cuspidaria** DC.
Sideropogon lasianthum (Bureau & K. Schum.) Pichon, = **Cuspidaria lasiantha** (Bureau & K. Schum.) L. G. Lohmann
Spathicalyx J. C. Gomes, = **Tanaecium** Sw.
Spathicalyx duckei (A. Samp.) A. H. Gentry, = **Tanaecium duckei** A. Samp.
Spathicalyx kuhlmannii J. C. Gomes, = **Tanaecium duckei** A. Samp.
Spathicalyx xanthophyllum (DC.) A. H. Gentry, = **Tanaecium xanthophyllum** (DC.) L. G. Lohmann
[*Spathodea* P. Beauv., Bignoniaceae, Tribe Oroxyleae]
Spathodea bracteosa DC., = **Adenocalymma bracteosum** (DC.) L. G. Lohmann
Spathodea candolleana Mart. ex DC., = **Neojobertia candolleana** (Mart. ex DC.) Bureau & K. Schum.
Spathodea corymbosa Vent., = **Bignonia corymbosa** (Vent.) L. G. Lohmann
Spathodea flaviflora Miq., = **Adenocalymma flaviflorum** (Miq.) L. G. Lohmann
Spathodea obovata Kunth, = **Martinella obovata** (Kunth) Bureau & K. Schum.
Spathodea podopogon DC., = **Fridericia podopogon** (DC.) L. G. Lohmann
Spathodea schomburgkii DC., = **Adenocalymma schomburgkii** (DC.) L. G. Lohmann
Spathodea uncata (Andrews) Spreng., = **Dolichandra uncata** (Andrews) L. G. Lohmann
Stenosiphanthus A. Samp., = **Fridericia** Mart.
Stenosiphanthus duckei A. Samp, = **Fridericia lauta** (Bureau & K. Schum.) L. G. Lohmann
Stizophyllum Miers
Stizophyllum cordifolium (DC.) Miers, = **Manaosella cordifolia** (DC.) A. H. Gentry
Stizophyllum inaequilaterum Bureau & K. Schum.
Stizophyllum perforatum (Cham.) Miers
Stizophyllum riparium (Kunth) Sandwith
[*Tabebuia* Gomes ex DC., Bignoniaceae, Tribe Crescentieae]
Tabebuia lanceolata DC., = **Mansoa lanceolata** (DC.) A. H. Gentry
Tabebuia japurensis DC., = **Fridericia japurensis** (DC.) L. G. Lohmann
Tabebuia latifolia (Rich.) DC., = **Callichlamys latifolia** (Rich.) K. Schum.
Tabebuia pyramidata (Rich.) DC., = **Tanaecium pyramidatum** (Rich.) L. G. Lohmann
Tabebuia xanthophylla DC., = **Tanaecium xanthophyllum** (DC.) L. G. Lohmann
Tanaecium Sw.
Tanaecium affine (A. H. Gentry) L. G. Lohmann
Tanaecium apiculatum A. H. Gentry
Tanaecium bilabiatum (Sprague) L. G. Lohmann
Tanaecium caudiculatum (Standl.) L. G. Lohmann
Tanaecium crucigerum Seem.
Tanaecium cyrtanthum (Mart. ex DC.) Bureau & K. Schum.
Tanaecium duckei A. Samp.
Tanaecium exitiosum Dugand
Tanaecium jaroba Sw.
Tanaecium mutabile (Bureau & K. Schum.) L. G. Lohmann
Tanaecium neobrasiliense L. G. Lohmann
Tanaecium nocturnum (Barb. Rodr.) Bureau & K. Schum., = **Bignonia nocturna** (Barb. Rodr.) L. G. Lohmann
Tanaecium pyramidatum (Rich.) L. G. Lohmann
Tanaecium revillae (A. H. Gentry) L. G. Lohmann
Tanaecium selloi (Spreng.) L. G. Lohmann
Tanaecium tetragonolobum (Jacq.) L. G. Lohmann
Tanaecium truncatum (A. Samp.) L. G. Lohmann
Tanaecium xanthophyllum (DC.) L. G. Lohmann
[*Tecoma* Juss., Bignoniaceae, Tribe Tecomeae]
Tecoma cyrtantha Mart. ex DC., = **Tanaecium cyrtanthum** (Mart. ex DC.) Bureau & K. Schum.
Tecoma hirta Mart. ex DC., = **Adenocalymma hirtum** (Mart. ex DC.) Bureau & K. Schum.
Tecoma lateriflora Mart.**, = **Cuspidaria lateriflora** (Mart.) DC.
Tecoma pratensis Bureau & K. Schum., = **Xylophragma pratense** (Bureau & K. Schum.) Sprague
Tecoma venusta (Ker Gawl.) Lem., = **Pyrostegia venusta** (Ker Gawl.) Miers

Tetrastichella Pichon, = **Cuspidaria** DC.
Tetrastichella inaequalis (DC. ex Splitg.) Pichon, = **Cuspidaria inaequalis** (DC. ex Splitg.) L. G. Lohmann
Tynanthus Miers
Tynanthus cognatus (Cham.) Miers
Tynanthus croatianus A. H. Gentry
Tynanthus elegans Miers
Tynanthus fasciculatus (Vell.) Miers
Tynanthus gondotiana, orth. var., = **Tynanthus goudotianus** (Bureau) Miers
Tynanthus goudotianus (Bureau) Bureau
Tynanthus guatemalensis Donn. Sm.
Tynanthus igneus Barb. Rodr., = **Pyrostegia venusta** (Ker Gawl.) Miers
Tynanthus hyacinthinus Standl., = **Bignonia hyancinthina** (Standl.) L. G. Lohmann
Tynanthus labiatus (Cham.) Miers
Tynanthus macranthus L. O. Williams
Tynanthus micranthus Corr. Méllo ex K. Schum.**
Tynanthus panurensis (Bureau) Sandwith
Tynanthus polyanthus (Bureau) Sandwith
Tynanthus pubescens A. H. Gentry
Tynanthus sastrei A. H. Gentry
Tynanthus schumannianus (Kuntze) A. H. Gentry
Tynanthus villosus A. H. Gentry
Tynnanthus, orth. var., = **Tynanthus** Miers
Urbaniella duseniana, orth. var., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Urbanolophium Melch., = **Amphilophium** Kunth
Urbanolophium dusenianum (Kraenzl.) Melch., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Urbanolophium glaziovii (Bureau ex K. Schum.) Melch., = **Amphilophium dusenianum** (Kraenzl.) L. G. Lohmann
Vasconcellia Mart., = **Fridericia** Mart.
Vasconcellia rego (Vell.) Mart., = **Fridericia rego** (Vell.) L. G. Lohmann
Vasconcellia sego (Vell.) Mart., = **Fridericia rego** (Vell.) L. G. Lohmann
[*Vitex* L., Lamiaceae]
Vitex bahiensis Schauer ex DC., = **Fridericia bahiensis** (Schauer ex DC.) L. G. Lohmann
Wunschmannia Urb., = **Amphilophium** Kunth
Wunschmannia staminea (Lam.) Urb., = **Amphilophium stamineum** (Lam.) L. G. Lohmann
Xylophragma Sprague
Xylophragma harleyi (A. H. Gentry ex M. M. Silva & L. P. Queiroz) L. G. Lohmann
Xylophragma heterocalyx (Bureau & K. Schum.) A. H. Gentry
Xylophragma myrianthum (Cham.) Sprague
Xylophragma platyphyllum (DC.) L. G. Lohmann
Xylophragma pratense (Bureau & K. Schum.) Sprague
Xylophragma seemannianum (Kuntze) Sandwith
Xylophragma xanthophylla (DC.) J. F. Macbr., = **Tanaecium xanthophyllum** (DC.) L. G. Lohmann
Xylophragma unifoliolatum J. F. Morales & Q. Jiménez

TAXONOMIC REVISION OF *GOUANIA* (RHAMNACEAE) FOR NORTH AMERICA[1]

Amy Pool[2]

Abstract

Taxonomic revision of *Gouania* Jacq. (Rhamnaceae) is presented for the full extent of its range in North America, from Florida and Mexico through Central America to and including Panama, and the islands of the Caribbean region, including the Bahamas. Fifteen species are recognized, five of which are described and published as new: *G. croatii* A. Pool (Panama and Colombia), *G. ferruginea* A. Pool (Guatemala and Honduras), *G. guiengolensis* A. Pool (Oaxaca, Mexico), *G. obamana* A. Pool (Mexico, Guatemala, Belize, and Honduras), and *G. pubidisca* A. Pool (Mexico, Guatemala, El Salvador, and Nicaragua). Lectotypes are designated for *Banisteria lupuloides* L. [≡ *G. lupuloides* (L.) Urb.] (and the synonymous *G. domingensis* L.), *G. colombiana* Suess., *G. glabriuscula* Stokes, *G. lupuloides* var. *aptera* Urb., *G. mexicana* Sessé & Moc., *G. mexicana* Rose [≡ *G. rosei* Wiggins], *G. paniculata* Spreng., *G. pubescens* Poir. var. *martinicensis* Poir., *G. pubescens* var. *pubescens*, *G. virgata* Reissek var. *virgata* [≡ *G. virgata* var. *guianensis* Reissek], *G. virgata* var. *brasiliensis* Reissek, and *Rhamnus polygama* Jacq. [≡ *G. polygama* (Jacq.) Urb.] (and the synonymous *G. tomentosa* Jacq.). Epitypes are designated for *B. lupuloides* L. [≡ *G. lupuloides*] (and the synonymous *G. domingensis* L.), *G. stipularis* DC., and *R. polygama* Jacq. [≡ *G. polygama*] (and the synonymous *G. tomentosa*). A neotype is selected for *R. domingensis* Jacq. and a lectotype is designated for the equivalent name *G. glabra* Jacq.

Resumen

Se presenta una revisión taxonómica de *Gouania* Jacq. (Rhamnaceae) en toda su extensión en América del Norte, desde Florida y México a través de América Central hasta e incluyendo Panamá, y las islas del Caribe incluyendo las Bahamas. Se reconocen 15 especies, cinco de las cuales se describen y publican como nuevas: *G. croatii* A. Pool (Panamá y Colombia), *G. ferruginea* A. Pool (Guatemala y Honduras), *G. guiengolensis* A. Pool (Oaxaca, México), *G. obamana* A. Pool (México, Guatemala, Belice y Honduras) y *G. pubidisca* A. Pool (México, Guatemala, El Salvador y Nicaragua). Se designan lectotipos para *Banisteria lupuloides* L. [≡ *G. lupuloides* (L.) Urb.] (y la sinónima *G. domingensis* L.), *G. colombiana* Suess., *G. glabriuscula* Stokes, *G. lupuloides* var. *aptera* Urb., *G. mexicana* Sessé & Moc., *G. mexicana* Rose [≡ *G. rosei* Wiggins], *G. paniculata* Spreng., *G. pubescens* Poir. var. *martinicensis* Poir., *G. pubescens* var. *pubescens*, *G. virgata* Reissek var. *virgata* [≡ *G. virgata* var. *guianensis* Reissek], *G. virgata* Reissek var. *brasiliensis* Reissek y *Rhamnus polygama* Jacq. [≡ *G. polygama* (Jacq.) Urb.] (y la sinónima *G. tomentosa* Jacq.). Se designan epitipos para *B. lupuloides* L. [≡ *G. lupuloides* (L.) Urb.] (y la sinónima *G. domingensis* L.), *G. stipularis* DC. y *R. polygama* Jacq. [≡ *G. polygama*] (y la sinónima *G. tomentosa*). Se selecciona un neotipo para *R. domingensis* Jacq. y se designa un lectotipo para el nombre equivalente *G. glabra* Jacq.

Key words: Bahamas, Caribbean, Central America, Florida, *Gouania*, IUCN Red List, Mexico, Neotropical Dry Forest, North America, Rhamnaceae, *Rhamnus*, Trinidad and Tobago.

Gouania Jacq. is a pantropical genus of approximately 50 species in the Rhamnaceae, a family of 52 genera and ca. 925 species (Medan & Schirarend, 2004). It can be distinguished from other Rhamnaceae by its tendriled lianescent habit and 3-winged dry schizocarps that separate into three 2-winged indehiscent mericarps (Medan & Schirarend, 2004). The genus was established by Jacquin in 1763 with two species from Haiti ("Domingensibus"), *G. tomentosa* Jacq. (previously published as *Rhamnus polygama* Jacq.; see *G. polygama* (Jacq.) Urb.) and *G. glabra* Jacq. (previously published as *R. domingensis* Jacq.; see *G. lupuloides* (L.) Urb.). *Gouania tomentosa* is indicated as the type species by Jacquin including the explanation of the derivation of the genus name (named for Antoine Goüan, 1733–1821, French botanist and medical doctor) in the description of *G. tomentosa* (Jacquin, 1763). The genus name was quickly adopted by other botanists, with Linnaeus in the same year (1763) publishing *G. domingensis* L., based on the same elements as his earlier (1753) published name, *Banisteria lupuloides* L. (see *G. lupuloides* (L.) Urb.).

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A number of names in *Gouania* were published subsequently over the next two centuries for taxa in North America, but no serious attempt was made to revise the North American species. Most North American floristic accounts (Standley, 1923; Standley & Steyermark, 1949; Liogier, 1953b; Fernández, 1986, 1996; Johnston, 2001; Acevedo-Rodríguez, 2003) have relied heavily on the degree of leaf pubescence, which has proved to be a very unreliable character. However, Reissek (1861), who provided a very detailed account for the South American species, recognized the importance of floral disc pubescence and the relative length of disc lobe to sepal length, using these characters to divide the species treated into three unnamed series: series I, with the floral disc entirely covered with trichomes; series II, with the trichomes of the floral disc restricted to the annulus; and series III, with the floral disc glabrous. Series III was subdivided into two subseries: IIIa, with disc lobes one half the length of the sepals; and IIIb, with disc lobes one fourth to one third the length of the sepals. Reissek (1861) also included stipules in his species descriptions and appears to be the first author to recognize that the stipules in some species are lobed (or semihastate in his terminology). Bornstein (1989) followed Reissek (1861) in using pubescence of the floral disc as an important character and added the shape of the mericarps to help separate the two species (*G. lupuloides* and *G. polygama*) found in the Lesser Antilles. Subsequently, two other publications (Liogier, 1994; Krings & Braham, 2005) also used these characteristics to separate *G. lupuloides* and *G. polygama*.

Morphology

Morphological characters are discussed below, and the most diagnostic of these are used in the comparison of *Gouania* species in Table 1.

BRANCHES

Bornstein (1989) found the degree of pubescence of the young branches to be helpful in separating *Gouania lupuloides* and *G. polygama* in the Lesser Antilles, but not in other geographic areas. I found young branch pubescence to be quite variable in degree and type for most species of *Gouania*. Exceptions to this are *G. colombiana* Suess. (puberulent to glabrous), *G. stipularis* DC. (glabrous), and *G. croatii* A. Pool, *G. ferruginea* A. Pool, and *G. velutina* Reissek (these three, densely villous or velutinous). A couple of species (*G. eurycarpa* Standl. and *G. obamana* A. Pool) have hollow young branches, but this is variable in a number of other species and might prove to be variable in these species as well.

LEAF BLADES

I found the most useful leaf character to be the number of lateral veins that lie on either side of the blade midrib. One side of the leaf often has one more lateral vein than the other; in this revision I have always used the higher number. The number of lateral veins per side of the midrib range from (two)three or four(five) in *Gouania hypoglauca* Standl. and three to five in *G. obamana* to (six)seven or eight(nine) in *G. croatii* and *G. polygama*, and seven or eight in *G. ferruginea* (see Table 1).

Another frequently useful leaf character is that the abaxial surface may dry lighter than the adaxial one. This difference is markedly so in *Gouania croatii*, *G. ferruginea*, *G. obamana*, *G. pubidisca* A. Pool, and *G. velutina*, and can be usually observed in *G. ekmanii* Alain, *G. hypoglauca*, and *G. polygama*. The leaves of *G. lupuloides*, *G. colombiana*, and *G. guiengolensis* A. Pool vary from markedly bicolored to unicolored.

In North America, the leaves of *Gouania* are nearly always distinctly toothed, and the teeth bear apical glands. The glands at the junction of the blade with the petiole are often elaborate and long-stipitate or sometimes borne on foliaceous appendages. These glands are extremely variable and were not found to be helpful in identifying species. The type and number of marginal teeth were also found to be too variable within a species to be helpful. I have tried to differentiate types of marginal tooth glands, but they are all very similar and not distinctive in North American specimens. This is not the case in South America, where some species, such as *G. trichodonta* Reissek and *G. riparia* Reissek, have the glands adorned with a tuft of trichomes while others, such as *G. alnifolia* Reissek, have very large and open glands.

Historically, the amount of leaf pubescence has been widely used to separate species of *Gouania*. I found both the type and quantity of leaf pubescence to be too variable in most species to be diagnostic. There are a few exceptions: *G. ekmanii* and *G. hypoglauca* have the abaxial blade surface densely covered between the veins with straight and tightly appressed trichomes 0.05–0.2 mm long. *Gouania colombiana* has the trichomes of the abaxial surface differentially retained mainly at the apex, but its leaves are otherwise nearly glabrous. The leaves of *G. stipularis* are always glabrous (or with trichomes restricted to the major venation), and those of *G. obamana* are also almost glabrous, with trichomes on the veins and in the axils of the lateral veins with the

Table 1. Comparison of North American Species of *Gouania*.

Morphological characters	*G. colombiana*	*G. conzattii*	*G. croatii*	*G. ekmanii*	*G. eurycarpa*	*G. ferruginea*	*G. guiengolensis*	*G. hypoglauca*	*G. lupuloides*	*G. obamana*	*G. polygama*	*G. pubidisca*	*G. rosei*	*G. stipularis*	*G. velutina*
Lateral veins per side	(4)5(6)	(5)6 to 8	(6)7 or 8(9)	5 or 6	4 or 5(6)	7 or 8	4 to 6	(2)3 or 4(5)	(3)4 or 5(6)	3 to 5	(6)7 or 8(9)	5 or 6 (7)	(4)5 to 7	(5)6(7)	5 to 7
Stipule lobes	1 or 2	2	2	2	2	2	1	1(2)	2	2	2	1(2)	1(2)	3	2
Shape of upper stipule lobe	ovate or reniform	lanceolate, acuminate	lanceolate, acuminate	lanceolate, acuminate	lanceolate, acuminate	lanceolate, acuminate	linear	triangular, acuminate	lanceolate, acuminate, or triangular	lanceolate, acuminate	lanceolate, acuminate	ovate, acute	lanceolate, acuminate	reniform	lanceolate, acuminate
Foliaceous lower stipule lobe	no	no	yes	no	no	no	no	no	variable	no	no	no	no	yes	yes
Pedicel length (mm)	1.25–2.5	0(−1)	0–0.5	1.25	0.75–2	0–0.75	0–1	0–0.25 (0.75)	(0.5)1–3 (−4)	0–1.5	0–1.5 (−2.5)	0–0.5	0–0.5 (0.75)	2–3.5	0–0.75
Disc lobe length relative to sepal length	3/4–1/1	1/4–1/3 (−1/2)	(1/3–) 1/2	1/3	1/4–1/3	(1/5–) 1/4	1/4–1/3 (−1/2)	1/6–1/3	1/5–2/5 (−1/2)	1/4–1/3 (1/2)	(1/3–)2/5–3/5 (−2/3)	1/5–1/3	1/3–2/5 (1/2)	1/10–1/4	(1/2–) 2/3–1/1
Disc surface pubescence	no	no	no	no	no	no	no	yes	no	no	no	yes	no	no	no
Disc annulus pubescence	no	variable	yes	yes	no	no	yes	yes	no	yes	yes	yes	variable	no	variable
Mericarp shape	butterfly	butterfly	dumbbell	butterfly	butterfly	butterfly	butterfly	butterfly	butterfly	dumbbell	dumbbell	butterfly	butterfly	butterfly	butterfly
Mericarp pubescence	no	no	yes	yes	yes	yes	no	yes	no	yes	no	yes	yes	no	yes
Fruit body height (mm)	6–10	5–6	3–4	4–5	(5) 6–9	6.2	5–6	6–12	4–7	4–6	(2.5–) 3–4	4–7	4–5	4–6	4–6
Mericarp wing height (mm)	11–13	7–10	6–7	6	(6) 8–11	7.2	6–7.5	9–14	(5) 6.6–12	(9–) 10–14	(4–) 5–8 (−9)	7–10	4–6	5–7	6–9
Mericarp width (mm)	10–17	12–15	12–15	8–9	11–15	12	7–8	10–15.3 (17)	(8) 9–16	14–20	(7–) 9–17	10–14	6–9	6–11	8–10 (11)
Fruit body width relative to mericarp width	1/6–1/4	1/3	1/6–1/4	1/4–1/3	1/4–1/3	2/5	3/5	1/4–1/2	(1/5) 1/4–1/2	1/5–1/4 (−1/3)	1/6–1/4 (−1/3)	1/5–1/3	(1/3) 1/2	1/3–1/2	1/4–1/3
Mericarp width relative to fruit body height	1.2–2.2	2–3	3–3.5	2	1.5–2	2	1–1.5	1.5–2	1.5–3.2	2.75–4	3–4(−5)	2–2.5	1.25–2	1–2	1.5–2 (−2.5)
Seed length (mm)	4	3.5–3.75	2–2.2	2.3–2.75	3–3.75	unknown	3.5–4	3.25–4.5	2.7–3.8	3.5	(1.8–) 2.2–2.75	2.5–3.25	2.5–3.5	3.1–3.5	2.25–2.5(3.3)

midrib. Abaxial leaf surfaces are always densely villous or tomentose in *G. croatii* and *G. ferruginea* and densely pilose to tomentose in *G. pubidisca* and *G. velutina*.

STIPULES

The stipules of Rhamnaceae are usually described as small (Medan & Schirarend, 2004) or small and generally deciduous (Standley & Steyermark, 1949; Nowicke, 1971) and have been largely ignored. However, the stipules of *Gouania* provide many useful characters (Table 1, Fig. 1). Most species of *Gouania* in North America have two well-developed stipule lobes, the upper lobe in most cases being lanceolate and acuminate (or sometimes triangular in *G. lupuloides*); however, one species, *G. stipularis*, has three well-developed stipule lobes, the two lateral lobes being foliaceous and reniform to orbicular and the mid-lobe lanceolate (Fig. 1H), and another species, *G. guiengolensis*, has unlobed linear stipules (Fig. 1B). *Gouania colombiana*, *G. hypoglauca*, *G. pubidisca*, and *G. rosei* Wiggins usually have only the upper stipule lobe developed (ovate to reniform in *G. colombiana* [Fig. 1A], triangular and acuminate in *G. hypoglauca*, ovate and acute in *G. pubidisca*, lanceolate and acuminate in *G. rosei*), but their stipules may at times also have a minute lower lobe. The lower stipule lobe is consistently foliaceous only in *G. croatii* (Fig. 9B), *G. stipularis*, and *G. velutina* (Fig. 1I), but can vary in *G. lupuloides* from subulate and 0.1 mm long to foliaceous and 14 mm long (Fig. 1C–G). The persistence of the stipules is also a good species-level character. They can be retained (usually) into or through fruiting in some species (*G. colombiana*, *G. ekmanii*, *G. eurycarpa*, *G. ferruginea*, *G. lupuloides*, *G. stipularis*, and *G. velutina*), or are lost in anthesis (*G. conzattii* Greenm., *G. croatii*, *G. guiengolensis*, *G. hypoglauca*, *G. pubidisca*, and *G. rosei*) or, in some species (*G. obamana* and *G. polygama*), before the leaves expand.

FLOWERS

All of the species of *Gouania* in North America have small (sepals 0.6–1.3 mm long) greenish yellow to greenish white flowers. The petals are all slightly smaller to equivalent to the sepals in length. The most diagnostic characters of the flowers (Table 1) are the relative pubescence of the floral disc, with the trichomes covering the whole disc excluding the lobes (series I of Reissek, 1861); with the trichomes along the annulus of the disc, through which the style protrudes at maturity (series II of Reissek, 1861); or with the disc totally glabrous (series III of Reissek, 1861). The length of the disc lobes, relative to the length of the sepals, distinguished subseries IIIa and IIIb for Reissek (1861). While these characters are useful, they must be used with caution. In North America, there are two species that usually have the entire nonlobed portion of the disc pubescent (*G. hypoglauca* and *G. pubidisca*, Fig. 13B), but sometimes have trichomes only around the annulus (at times with rays extending onto the disc proper). Some species have the annulus and only the annulus with trichomes (*G. croatii*, Fig. 9D; *G. ekmanii*, *G. guiengolensis*, Fig. 11C; *G. obamana*, Fig. 12C; and *G. polygama*), while other species may have the annulus pubescent or not (*G. conzattii*, *G. rosei*, and *G. velutina*). The length of the disc lobes relative to the length of the sepals varies from one tenth in *G. stipularis* to being equivalent in *G. colombiana* and *G. velutina*. The relative pubescence of the discs is observable even in very young, pried-open buds and, along with the relative disc lobe/sepal length, can also usually be observed in fruit. Pedicel length is a problematic character because in most of the species, the pedicels expand as the flowers mature.

MERICARPS

The fruits of *Gouania* consist of three 2-winged mericarps that separate at maturity (Fig. 2A–N). The relative shape of the mericarps, as well as their dimensions, external pubescence (Table 1), and coloration patterns on the inner surface, are all diagnostic characters. In North America, the mericarps are two basic shapes. What I refer to as dumbbell-shaped mericarps are transversely oblong with a very broad sinus at the apex and base of the fruit body (Fig. 2C, J) or only at the apex in *G. obamana* (Fig. 2I). The fruit body itself is like the central bar or handhold of a dumbbell. Bornstein (1989: 165) described this fruit shape as "fruit wing attached to side of fruit body only," and I borrow his description. This is not technically accurate, as a thin margin of the wing continues along the apex and base of the fruit body, but it does help to explain the shape. What I term as butterfly-shaped mericarps are more or less circular to transversely oblong, with emarginations to deep clefts at the apex and base of the fruit body (Fig. 2A, B, D–H, K–M) or emargination only at the base in *G. velutina* (Fig. 2N). Bornstein (1989: 165) described this type as "fruit wing attached to side and base, and/or apex of fruit body," and I again borrow from him. For the mericarps of each species, I give measurements for the height of the fruit body (i.e., the middle part containing the seed), the height of the wings, the

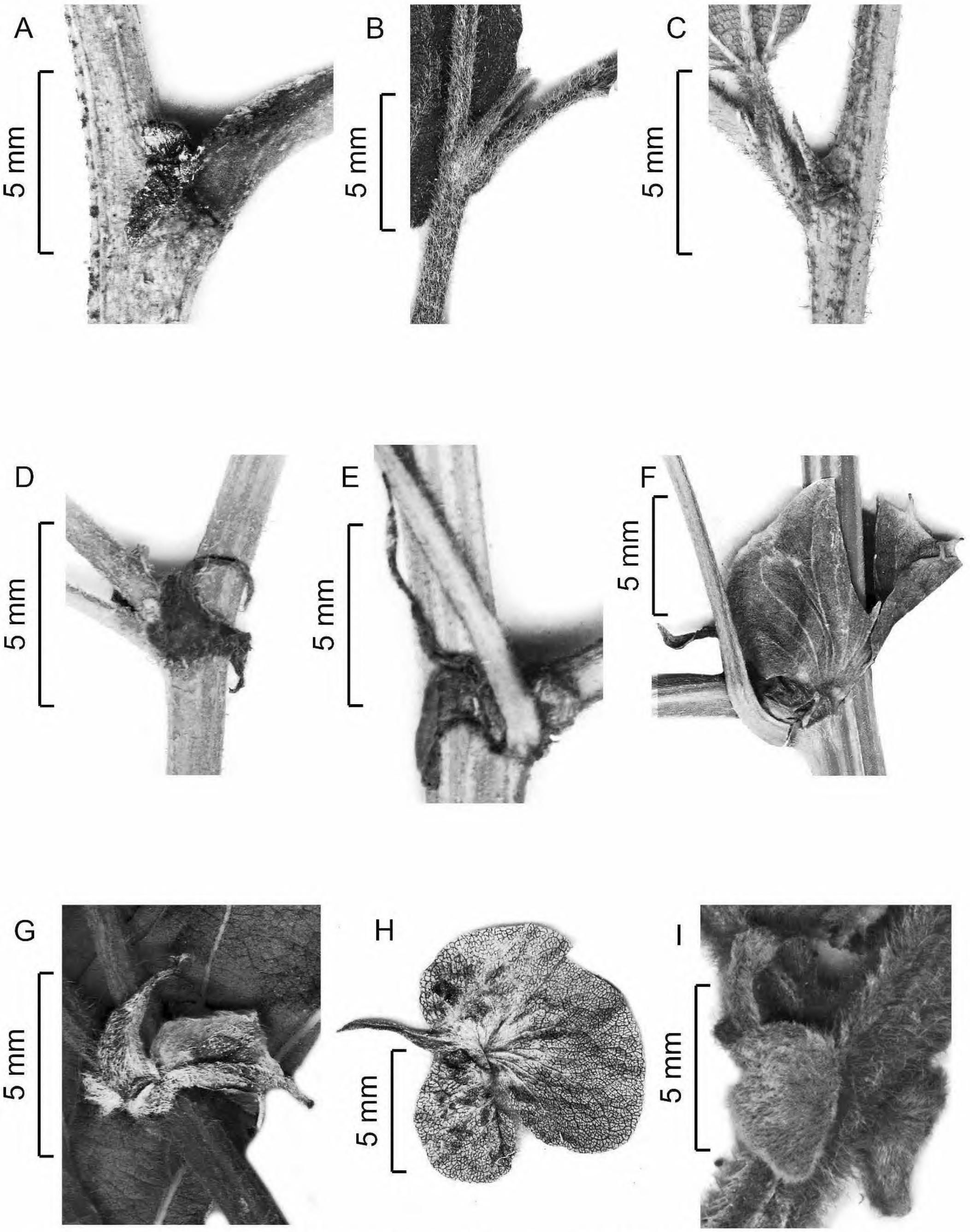


Figure 1. Stem nodes with stipules of selected species of *Gouania*. —A. Unlobed, ovate stipule of *G. colombiana* Suess., scanned from *J. A. González et al. 1640* (MO). —B. Unlobed, linear stipule of *G. guiengolensis* A. Pool, scanned from the paratype *E. Matuda 586* (MO). C–G. Variability in bilobed stipules of *G. lupuloides* (L.) Urb. —C. Stipule with upper lobe triangular, acuminate, firm and lower lobe subulate in *G. lupuloides*, scanned from *D. E. Breedlove & G. Davidse 54431* (MO). —D. Stipule with upper lobe lanceolate, acuminate and the tip long extended and flexuous and lower lobe lanceolate and acuminate in *G. lupuloides*, scanned from *E. F. Cabrera C. & H. de Cabrera 9460* (MO). —E. Stipule with upper lobe lanceolate, acuminate and the tip long extended and flexuous and lower lobe foliaceous and ovate without teeth in *G lupuloides*, scanned from *H. S. Gentry 4949* (MO). —F. Stipule with upper lobe lanceolate, acuminate and the tip long extended and flexuous and lower lobe foliaceous and reniform with three short glandular teeth in *G. lupuloides*, scanned from *J. I. Calzada 1684* (MEXU). —G. Stipule with upper lobe lanceolate, acuminate and the tip long extended and flexuous and lower lobe foliaceous and ovate with three long-extended glandular teeth in *G. lupuloides*, scanned from *R. Torres C. et al. 3560* (MO). —H. Stipule with three well-developed lobes of *G. stipularis* DC., scanned from *O. Téllez V. & F. Chiang C. 9718* (MO). —I. Bilobed stipule, with the lower lobe foliaceous and cucullate of *G. velutina* Reissek, scanned from *E. López 82* (MO).

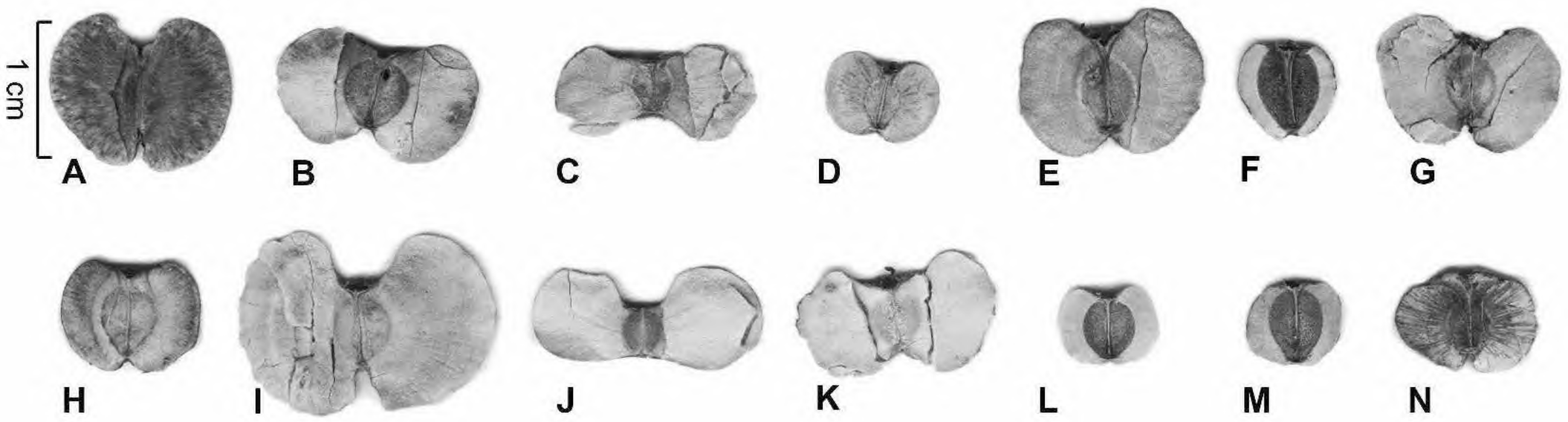


Figure 2. Inner surfaces of mericarps of North American *Gouania* Jacq. (excluding *G. ferruginea* A. Pool). —A. *Gouania colombiana* Suess. (*G. C. de Nevers & H. Herrera 4269*, MO). —B. *Gouania conzattii* Greenm. (*T. B. Croat 45467*, MO). —C. *Gouania croatii* A. Pool (from the paratype *T. B. Croat 13482*, MO). —D. *Gouania ekmanii* Alain (*A. Liogier 6862*, PR). —E. *Gouania eurycarpa* Standl. (*C. Chan V. 4573*, MO). —F. *Gouania guiengolensis* A. Pool (from the paratype *M. L. Torres C. et al. 580*, MO). —G. *Gouania hypoglauca* Standl. (*P. P. Moreno 12408*, MO). —H. *Gouania lupuloides* (L.) Urb. (*S. P. Darwin et al. 2170*, MO). —I. *Gouania obamana* A. Pool (from the paratype *G. Ibarra Manríquez & S. Sinaca C. 3084*, MO). —J. *Gouania polygama* (Jacq.) Urb. (*E. M. Martínez S. et al. 35165*, MO). —K. *Gouania pubidisca* A. Pool (from the paratype *W. D. Stevens & O. M. Montiel J. 33195*, MO). —L. *Gouania rosei* Wiggins (*R. Moran 19034*, MO). —M. *Gouania stipularis* DC. (*Y. Mexía 8887*, MO). —N. *Gouania velutina* Reissek (*R. L. Liesner 4338*, MO).

distance between the highest points of the two wings, the width of the mericarp, and the width of the fruit body. Relative width of the mericarp to height of the fruit body as well as width of the fruit body to width of the mericarp is also given. The two shapes can also be defined by relative measurements: in dumbbell-shaped mericarps, the width across the entire mericarp is 2.5–4(–5) times the height of the fruit body and (rarely, or) the distance between the highest points of the two wings of the mericarp usually 1.5–3 times the height of the fruit body, whereas in butterfly-shaped mericarps the width across the entire mericarp is 1–2.8(–3.2) times the height of the fruit body and the distance between the highest points of the two wings of the mericarp $\leq$ 1(–1.5) times the height of the fruit body. For most of the North American species with butterfly-shaped mericarps, the width of the mericarp is only to twice the height of the fruit body. The only exceptions are *G. conzattii* (Fig. 2B, 2–3 times), *G. lupuloides* (Fig. 2H, 1.5–3.2 times), and *G. pubidisca* (Fig. 2K, 2–2.5 times), and in *G. lupuloides* and *G. pubidisca* the distances between the highest points of the two wings of the mericarp are less than to equal to the height of the fruit body. However, *G. conzattii* measures ca. 1.5 times the height of the fruit body, and its mericarps are therefore somewhat intermediate between the two types. In North America, only *G. croatii* (Fig. 2C), *G. obamana* (Fig. 2I), and *G. polygama* (Fig. 2J) have dumbbell-shaped mericarps. Unfortunately, the mericarp wings of all species of *Gouania* develop late in the ontogeny of the fruit, and wingless immature fruits may open in the press and appear to have nearly mature seeds. Mericarps vary in size from a fruit body height of 3 mm in *G. croatii* (Fig. 2C) and *G. polygama* (Fig. 2J) to 12 mm in *G. hypoglauca* (Fig. 2G), and mericarp width ranges from 6 mm in *G. rosei* (Fig. 2L) and *G. stipularis* (Fig. 2M) to 20 mm in *G. obamana* (Fig. 2I).

The two most common and widely distributed species of *Gouania* in North America have glabrous or nearly glabrous mericarps, one (*G. polygama*) dumbbell-shaped and one (*G. lupuloides*) butterfly-shaped. However, most of the species in our area have persistently pubescent mericarps: *G. croatii*, *G. ekmanii*, *G. eurycarpa*, *G. ferruginea*, *G. hypoglauca*, *G. obamana*, *G. pubidisca*, *G. rosei*, and *G. velutina* (as noted in Tables 1–4). All species of *Gouania* in North America have more or less pubescent hypanthia, and the young fruits have some trichomes. However, in species with nearly glabrous mature mericarps, the very young developing fruits are usually sparsely pilose (sparsely puberulent in *G. colombiana*, sometimes sparsely sericeous in *G. lupuloides*, rarely abundantly pilose in *G. polygama*). The very young fruits of most species with persistently pubescent mature mericarps are densely velutinous and resemble miniature pompom balls with trichomes at right angles to the surface (Fig. 9E, 10B, 13C; those of *G. hypoglauca* sometimes tomentose and of *G. rosei* sometimes pilose).

Fruits of most North American *Gouania* species have no notable coloration patterns on the internal surfaces of the mericarps. The wings and fruit body are more or less the same pale color or the fruit body is slightly darker. Notable exceptions are *G. guiengolensis* (Fig. 2F) and *G. rosei* (Fig. 2L), the fruit bodies of which dry dark red-brown and contrast sharply with the pale wings. The fruit body of *G. stipularis* (Fig. 2M) usually dries medium to dark

Table 2. Distribution of *Gouania* Jacq. in Mexico, by state. *Gouania* species with pubescent mericarps are indicated in boldface.

	G. conzattii	***G. eurycarpa***	*G. guiengolensis*	*G. lupuloides*	***G. obamana***	*G. polygama*	***G. pubidisca***	***G. rosei***	*G. stipularis*	***G. velutina***
Baja								X		
Sonora								X		
Chihuahua				X				X		
Sinaloa				X				X		
Nayarit	X			X			X	X	X	
Jalisco	X			X				X	X	
Colima	X							X	X	
Michoacán				X				X	X	
Guerrero	X			X			X	X	X	
Oaxaca	X		X	X	X	X	X	X	X	X
Chiapas		X		X	X	X	X			
Durango				X						
México	X			X					X	
Morelos				X						
Tamaulipas				X						
San Luis Potosí				X		X				
Querétaro				X		X				
Hidalgo				X		X				
Tlaxcala	X									
Puebla	X			X	X	X				
Veracruz				X	X	X				
Tabasco				X	X	X				
Campeche	X			X		X				
Yucatan	X			X						
Quintana Roo	X			X						

brown, in strong contrast to the wings. The fruit body of *G. velutina* (Fig. 2N) dries grayish red-brown with distinctive rays extending into the wings. Faint rays in the wings can be seen in *G. croatii*.

Reproductive Biology

There are numerous references to polygamy in the genus *Gouania* (e.g., Standley & Steyermark, 1949; Nowicke, 1971; Medan & Schirarend, 2004). However, in North America, the species all appear to bear only perfect flowers that are protandrous. The stamens are first released from the enclosing petals and the anthers dehisce. The pistillate phase then begins (usually not until after the pollen has been released) with the exsertion of the style through the annulus of the floral disc.

Mericarp Dispersal

The assumption is that the winged mericarps of *Gouania* are wind-dispersed (Ridley, 1930). Medan

Table 3. Distribution of *Gouania* Jacq. in Central America (excluding Mexico). *Gouania* species with pubescent mericarps are indicated in boldface.

	G. colombiana	***G. croatii***	***G. eurycarpa***	***G. ferruginea***	***G. hypoglauca***	*G. lupuloides*	***G. obamana***	*G. polygama*	***G. pubidisca***	***G. velutina***
Guatemala			X	X		X	X	X	X	
Belize			X			X	X	X		
El Salvador						X		X	X	
Honduras			X	X		X	X	X		
Nicaragua					X	X		X	X	
Costa Rica	X				X	X		X		X
Panama	X	X			X	X		X		X

Table 4. Distribution of *Gouania* Jacq. in Florida and the islands of the Caribbean region. *Gouania* species with pubescent mericarps are in boldface.

	G. ekmanii	*G. lupuloides*	*G. polygama*	***G. velutina***
Florida		X		
Bahamas		X		
Cuba	X	X	X	
Jamaica		X		
Hispaniola		X	X	
W Puerto Rico		X	X	
E Puerto Rico	X			
Lesser Antilles excluding Grenada, St. Vincent, and Barbados	X			
St. Vincent	X		X	
Grenada	X		X	
Barbados	X			
Tobago			X	
Trinidad			X	X

(1989) studied, using scanning electron microscopy, the dissected mericarps of six species of *Gouania*, including one North American species (*G. polygama*) with dumbbell-shaped mericarps and two (*G. colombiana* and *G. lupuloides*) with butterfly-shaped mericarps. All have the majority of the wing tissue made up of parenchymatous cells that are apparently filled with air at fruit maturity (Medan, 1989), presumably making the mericarps lighter. The rate of descent was studied only for *G. polygama*, the mericarps of which were found to spin tightly around a vertical line before a period of free descent, similar to the fruits of wind-dispersed species in other taxa. However, it is possible that water dispersal may also be relevant. One mericarp of each North American species (excluding *G. ekmanii* and *G. ferruginea*) was placed in a beaker of water on my desk. The time the mericarps stayed afloat varied from ca. 24 hours (*G. croatii*, *Croat 7984*; *G. rosei*, *Castrejón R. et al. 976*; *G. stipularis*, *Mexía 8887*) to 24 days (*G. colombiana*, *de Nevers & Herrera 4269*; *G. guiengolensis*, *Torres C. et al. 238*). This preliminary survey did not show any pattern suggesting a relationship between mericarp shape, pubescence, or relative fruit body and mericarp sizes to floatability. However, the capacity to stay afloat for up to 24 days with no damage to the mericarp or seed clearly suggests that water might play a role in dispersal.

Geographic Distribution

Tables 2 through 4 categorize the geographic distributions of the North American species of *Gouania* by Mexican state (Table 2), Central American country (Table 3), and Caribbean region islands (and Florida) (Table 4). The known distributions of the species are mapped on Figures 3 through 8. *Gouania* species are very commonly collected, and the maps should reflect fairly accurately their true distributions. Most of the species are found primarily in dry to very dry habitats from 0 to 1000 m elevation. Exceptions to this are *G. colombiana* (Fig. 6A), *G. croatii*, and *G. hypoglauca* (both, Fig. 6B), which are found in wet to very wet evergreen forests. *Gouania obamana* (Fig. 4A) is found only in evergreen forests, and *G. polygama* (Figs. 4B, 7B, 8B) is usually found in evergreen and sub-evergreen forests from 0 to 500 m, but sometimes is found in dry forest to 1200 (rarely to 1800) m. *Gouania lupuloides* (Figs. 3, 7A, 8A) is usually found in dry thickets, oak forests, and deciduous to sub-deciduous forests from 0 to 1700 m, but is sometimes found in sub-evergreen to evergreen forests. *Gouania eurycarpa* (Figs. 3, 5B) is found in sub-deciduous to sub-evergreen forests, apparently in wetter habitats than *G. lupuloides*, as illustrated by their relative distributions on the Yucatan Peninsula (Fig. 3). *Gouania conzattii* (Fig. 3) and *G. ferruginea* (Fig. 5B) are found only at higher elevations (1500–2200 m) than most species of *Gouania*, in oak, oak-pine, or *Liquidambar* L. forests. *Gouania rosei* (Fig. 5A) and *G. velutina* (Fig. 5A, 6A, 8A) are probably found in the driest habitats, the former in sub-deciduous, deciduous, and thorn forests and the latter in savanna and dry shrub land. *Gouania polygama* and *G. lupuloides* have overlapping geographic distributions in most of the Caribbean Islands. However, *G. polygama* (Fig. 8B) is absent from Jamaica, eastern Puerto Rico, and all but the southernmost islands of Lesser Antilles, but is present in Trinidad and Tobago, while *G. lupuloides* (Fig. 8A) is present in Jamaica, all of Puerto Rico and all of the Lesser Antilles, but absent from Trinidad and Tobago.

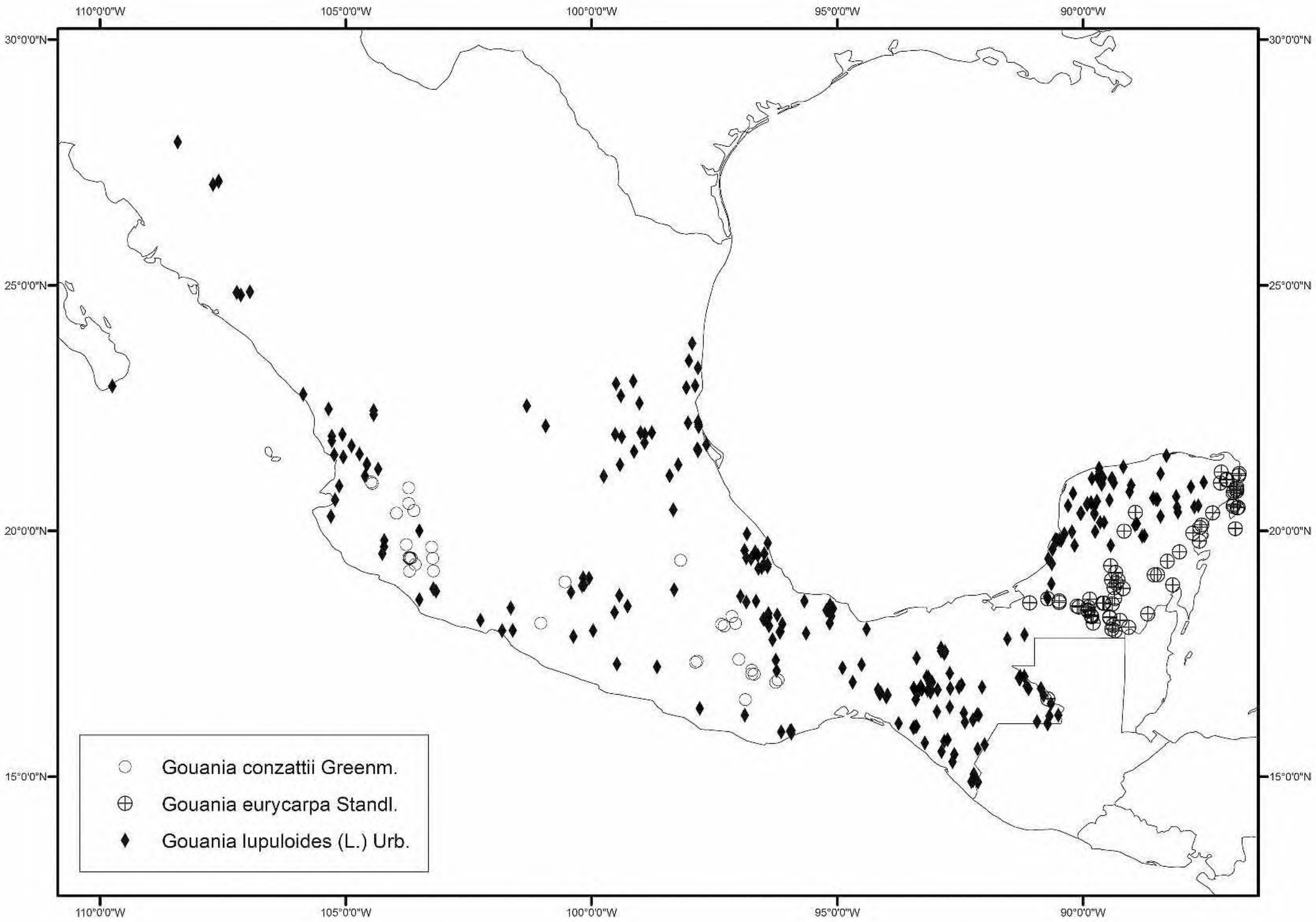


Figure 3. Geographic distribution of *Gouania conzattii* Greenm., across its known distributional range. Geographic distribution of *G. eurycarpa* Standl. and *G. lupuloides* (L.) Urb. in Mexico. See also the mapped distributions for *G. eurycarpa* in Central America (Fig. 5B) and *G. lupuloides* in Central America (Fig. 7A) and in the Caribbean region (Fig. 8A).

The vegetation-type patterns cited above (and in the taxonomic portion of this paper) are based on herbarium labels. As the highest diversity of species is found in Pacific to central Mexico, it is interesting to compare the species distribution maps in Mexico (excluding the widespread *Gouania lupuloides* and *G. polygama*) to the vegetation zones depicted on the "Mapa Esquemático de la Vegetación de México" of Rzedowski (1981: fig. 179). There are good correlations, and what seem to be oddly spotty species distributions actually follow the mosaic of vegetation types. Vegetation types for each Mexican species (excluding *G. lupuloides* and *G. polygama*), following Rzedowski (1981: fig. 179), are: *G. conzattii*, "bosque de coniferas y de quercas"; *G. eurycarpa*, "bosque tropical perennifolio"; *G. guiengolensis*, "bosque tropical caducifolio"; *G. obamana*, "bosque tropical perennifolio"; *G. pubidisca*, "bosque tropical subcaducifolio," with a few collections in "bosque tropical caducifolio"; *G. rosei*, "matorral xerofilo" and "bosque espinoso," with a few collections in "bosque tropical caducifolio"; *G. stipularis*, "bosque espinoso," "bosque tropical caducifolio," and "bosque tropical subcaducifolio"; and *G. velutina*, "bosque espinoso." Given the frequency of *Gouania* collections and the habitat specificity of most species (excluding *G. lupuloides* and *G. polygama*), it is suggested that *Gouania* species might be used as indicators to follow climate-based changes in vegetation.

Materials and Methods

All specimens examined as part of this study have been incorporated into the Missouri Botanical Garden database-management system TROPICOS, <http://www.tropicos.org/>, which now contains label information for all Western Hemisphere *Gouania* specimens housed at MO, in addition to those received on loan from A, B, BM, CAS, F, G, GH, K, M, MEXU, MICH, MSB, NY, PR, TEX, and US. Specimens determined by the author were selected from this database to generate the numbered exsiccatae (Appendix 1) and the distribution maps, the latter with the assistance of Burgund Bassüner. Dots on the maps (Figs. 3–8) represent a majority of the specimens examined by the author, including specimens with geographic coordinates provided on collection labels and those for which the author was able to estimate the geographic coordinates. These same coordinates were used by Bassüner to deter-

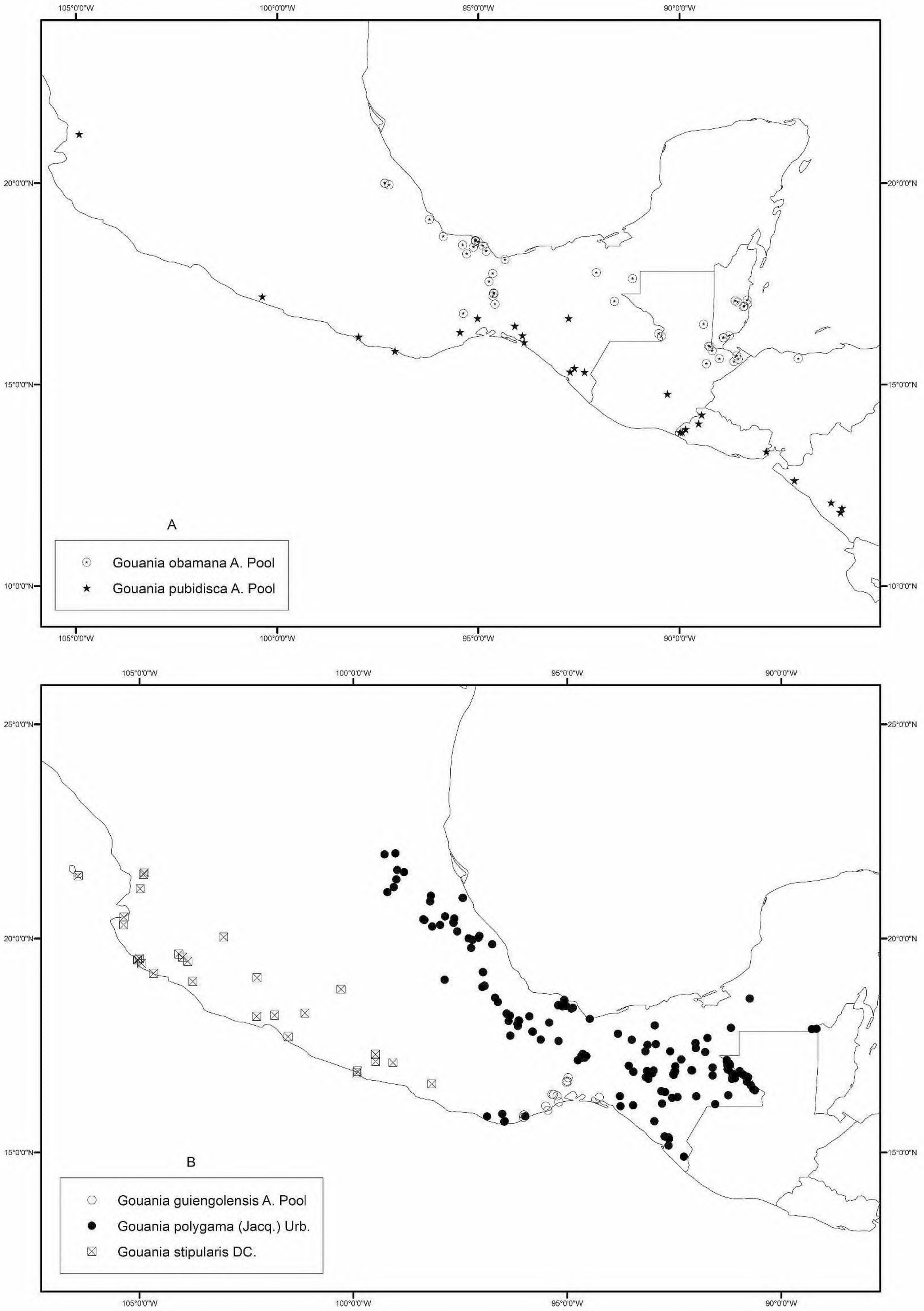


Figure 4. —A. Geographic distribution of *Gouania obamana* A. Pool, across its known distributional range. Geographic distribution of *G. pubidisca* A. Pool across its known distributional range. —B. Geographic distribution of *G. guiengolensis* A. Pool across its known distributional range. Geographic distribution of *G. polygama* (Jacq.) Urb. in Mexico. See also the mapped distributions for *G. polygama* in Central America (Fig. 7B) and in the Caribbean region (Fig. 8B). The distribution of *G. polygama* across South America is not mapped. Geographic distribution of *G. stipularis* DC. across its known distributional range.

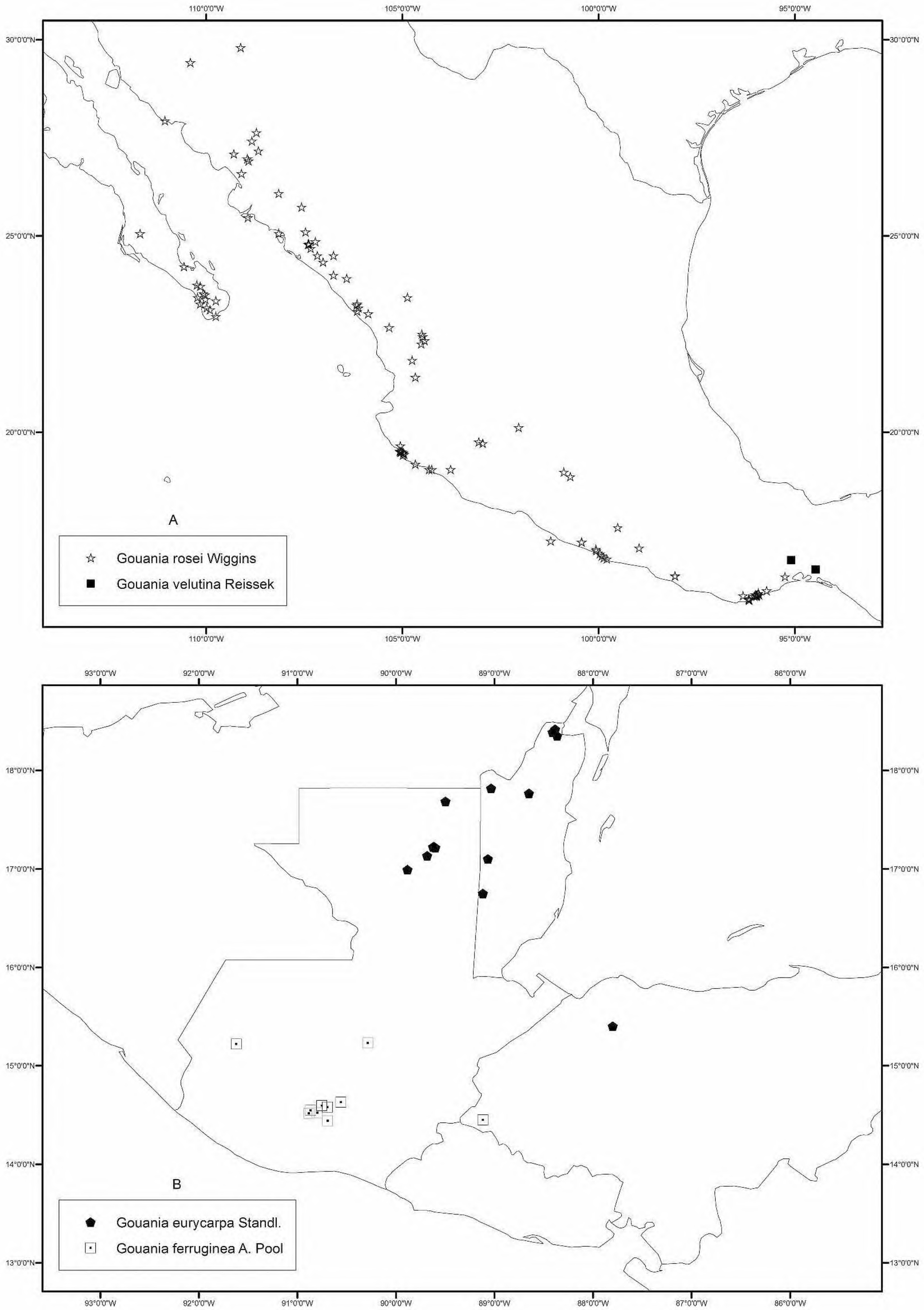


Figure 5. —A. Geographic distribution of *Gouania rosei* Wiggins, across its known distributional range. Geographic distribution of *G. velutina* Reissek in Mexico. See also the mapped distributions for *G. velutina* in Central America (Fig. 6A) and in the Caribbean region (Fig. 8A). Specimens of *G. velutina* from South America are not mapped. —B. Geographic distribution of *G. eurycarpa* Standl. in Central America. See also the mapped distributions for *G. eurycarpa* in Mexico (Fig. 3). Geographic distribution of *G. ferruginea* A. Pool across its known distributional range.

mine species occupancy extent and occupancy area. Locality information for specimen citations has been truncated; more specific locality data are available at the TROPICOS website.

In the following descriptions, tooth glands described are those above the leaf blade base.

The shape of the mericarp is very helpful in distinguishing the species of *Gouania* (Fig. 2A–N). To help define the shape of mericarps, the following measurements were made: height of fruit body, height of mericarp wing, distance between highest points of two wings, width of mericarp, and width of fruit body.

An attempt has been made to determine conservation status for each taxon based on IUCN (2012) criteria. However, these estimates are based only on estimated occupancy, area, and extent, which themselves are based on herbarium specimens, many of which were geo-referenced after the fact based on vaguely recorded collection localities. In addition, for most of the species of *Gouania* treated here, the extents of occupancy are useless because the distribution polygons include large areas of ocean. Changes in occupancy (Bb, c), potential threats, and area size affected by threats (criteria for IUCN size of location Ba), population reduction (A), and number of mature individuals (C, D) are not known for any of the taxa treated here. As many of the species are known only from dry forests, further study is strongly recommended to determine their conservation status. Extent and area of occupancy and area of occupancy outside protected areas were all calculated by Bassüner.

Taxonomic Treatment

Gouania Jacq., Select. Stirp. Amer. Hist. 263. 1763.
TYPE: *Gouania tomentosa* Jacq.

Lianas or scandent shrubs, climbing by circinate tendrils that originate from axils of leaves, especially those subtending inflorescences or terminating axillary branches, or cyme bracts, unarmed. Leaves alternate, petiolate; glands at junction of leaf and petiole frequently stipitate or foliaceous; dentate, each tooth with an apical gland; stipules present, often persistent, unlobed or more frequently 2(3)-lobed. Inflorescences axillary or terminal, racemiform or paniculate thyrses composed of small, multiflowered cymes, the cymes subtended by bracts; peduncles of cymes usually very short, pedicels elongating as flowers mature. Flowers bisexual (in North America, reportedly [Medan & Schirarend, 2004] sometimes unisexual by abortion, the plants polygamous, not observed), 5-merous; hypanthium shallowly obconical to campanulate, adhering to the ovary; sepals triangular, valvate in bud, adaxially keeled, persistent; petals usually smaller than or equal to sepals in length, strongly concave, short-clawed, apically rounded to bifid, white or greenish white, enfolding the stamens, deciduous; stamens opposite petals, the filaments linear to narrowly triangular, adnate to base of petals; anthers dehiscing by longitudinal slits; disk broadly annular, epigynous, fleshy, nectiferous, glabrous or pubescent (the trichomes sometimes restricted to the annulus), with 5 lobes (possibly of staminodial origin) opposite the sepals (rarely unlobed), the lobes entire or apically 2- or irregularly lobed; ovary inferior, 3-locular; style trifid, usually exerted through disc annulus after stamen dehiscence; stigmas 3, small. Fruit a dry schizocarp, 3-winged at maturity, separating septicidally into three 2-winged mericarps, each of which remains temporarily attached apically and suspended from 2 carpophores; mericarps indehiscent, 1-seeded, the external surface usually initially with some trichomes, at maturity densely pubescent or glabrescent, internally drying sometimes with darker pigmentation over fruit body, coloration sometimes extending by ray-like projections onto wings; seeds ellipsoid, slightly ventrally concave and dorsally convex, often shiny brown.

Key to Species of *Gouania* of North America, from Florida and Mexico to Panama and the Islands of the Caribbean Region

1a. Fruits glabrous or with few trichomes over fruit bodies only (rarely with few trichomes on wings in *G. polygama*).
  2a. Fruit mericarps dumbbell-shaped, the wings attached ± to the sides of fruit body only, height of fruit body (2.5–)3–4 mm, the width across the entire mericarp 3–4(–5)× height of fruit body and (rarely, or) distance between highest points of 2 wings of mericarp usually 2–3× height of fruit body; annulus of disc pubescent, the disc lobes variable in shape (often lanceolate, acuminate), frequently apically tapering, (1/3–)2/5–3/5 (–2/3) length of sepals ..... 11. *G. polygama*
  2b. Fruit mericarps butterfly-shaped, the wings attached to apex and base of fruit body as well as sides, height of fruit body 4–10 mm, the width across the entire mericarp 1–2.8(–3.2)× height of fruit body and distance between highest points of 2 wings of mericarp ≤ 1(–1.5)× fruit body height; annulus of disc glabrous or, if pubescent, the disc lobes generally square or transversely rectangular, rarely apically tapering, (1/4–)1/3 (–1/2) length of sepals.
    3a. Disc lobes lanceolate, acuminate, 3/4–1× length of sepals; leaves nearly glabrous with concentration of minute appressed trichomes at apex; mature mericarps with fruit body height 6–10 mm, fruit body width 1/6–1/4 mericarp width; Costa Rica to South America ..... 1. *G. colombiana*

3b. Disc lobes usually square or transversely rectangular and not apically tapering, 1/10–2/5(–1/2) length of sepals; leaves variously pubescent, but not with trichomes distributed as above; mature mericarps with fruit body height 4–7 mm, fruit body width (1/5–)1/4–3/5 mericarp width; Mexico to Panama and West Indies.

4a. Stipules 3-lobed (with 2 large lateral rounded lobes and 1 central narrow lanceolate, acuminate lobe), usually at least some retained into fruit; disc lobes 1/10–1/4 length of sepals ... 14. *G. stipularis*

4b. Stipules unlobed or bilobed (sometimes with large glandular teeth in *G. lupuloides*), rapidly caducous to retained in fruit; disc lobes (1/6–)1/5–2/5(–1/2) length of sepals.

5a. Stipules unlobed, linear, usually lost in flower; internal surface of mature mericarps with fruit body drying dark red-brown and strongly contrasting with wings, width of fruit body 3/5 width of mericarp, width of mericarp 1–1.5× height of fruit body; annulus of disc with some trichomes; Mexico, Isthmus of Tehuantepec, mainly on or near Cerro Guiengola, at 30–720 m elevation ..... 7. *G. guiengolensis*

5b. Stipules bilobed, the lobes variously shaped (but at least one lanceolate, acuminate, or narrowly triangular), usually at least some retained in fruit; internal surface of mature mericarps with fruit body drying only slightly or moderately darker than wings, width of fruit body 1/5–1/2(–3/5) width of mericarp, width of mericarp 1.5–3.2× height of fruit body; annulus of disc glabrous or, if with trichomes, then from Mexico, Nayarit to northern Oaxaca and (400)1000–2300 m elevation.

6a. Lateral leaf veins (5)6 to 8 per side of midrib; flowers sessile (rarely with pedicels to 1 mm); hypanthium and sepals densely villous, hypanthium drying with white trichomes, sepals with ferruginous or ferruginous and white trichomes; annulus glabrous or pubescent; distance between highest points of 2 wings of mericarp 7–10 mm, 1/2–3/4 width of entire mericarp; western and central Mexico, (400)1000–2200 m elevation; flowering May to October, peaking June to August ..... 2. *G. conzattii*

6b. Lateral leaf veins (3)4 to 6 per side of midrib; flowers with pedicels (0.5–)1–3(–4) mm; hypanthium and sepals sparsely to densely sericeous or (rarely) tomentose, drying with trichomes concolorous, from white to red-brown or ferruginous; annulus glabrous; distance between highest points of 2 wings of mericarp 3–7 mm, (1/4–)1/3–1/2(–3/5) width of entire mericarp; southern Florida, Mexico to Panama and West Indies, 0–1700(–2300) m elevation; flowering (rarely July) August to February (rarely March to May), peaking in September and October where sympatric with *G. conzattii* ..... 9. *G. lupuloides*

1b. Fruits densely pubescent with numerous trichomes on fruit bodies and wings.

7a. Disc (excluding, or often including, lobes) entirely covered with trichomes, or trichomes around annulus and extending in numerous rays from annulus onto disc (rarely only around annulus in *G. hypoglauca*).

8a. Abaxial surface of leaves totally covered between venation with trichomes to 0.1 mm long (rarely lost with age), only visible at 20× magnification, tightly appressed; lateral veins (2)3 or 4(5) per side of the blade midrib; fruits tomentose with trichomes 0.05–0.25 mm, fruit body 6–12 mm high; southeast Nicaragua to Panama, flowering May to September ..... 8. *G. hypoglauca*

8b. Abaxial surface of leaves densely pilose to tomentose (though not totally covered between venation) with trichomes 0.25–0.75 mm, visible at 10× magnification, not tightly appressed; lateral veins 5 or 6(7) per side of the blade midrib; fruits pilose to velutinous with trichomes 0.25–0.5 mm, fruit body 4–7 mm high; western Mexico and Central America, Mexico to Nicaragua (Granada), flowering August to February ..... 12. *G. pubidisca*

7b. Disc entirely glabrous or with trichomes restricted to annulus.

9a. Disc lobes lanceolate, acuminate, (1/2–)2/3–1× length of sepal lobes, the annulus glabrous (rarely with a few trichomes in Trinidad); stipules with the lower lobe ± orbicular or broadly reniform, usually retained into fruit; mature mericarps modified butterfly-shaped, the apex truncate or nearly so ..... 15. *G. velutina*

9b. Disc lobes square or transversely rectangular to lanceolate, acuminate, (1/5–)1/4–1/2 length of sepal lobes, the annulus glabrous or pubescent; stipules without an orbicular lobe, the lower lobe reniform only in *G. croatii* and then usually lost early; mature mericarps butterfly- or dumbbell-shaped, the apex with an emargination, cleft or broad sinus.

10a. Fruit mericarps dumbbell-shaped, the wings attached ± to the sides of fruit body only or to the sides and base, width across the entire mericarp 2.5–4× the height of the fruit body and distance between highest points of 2 wings of mericarp 1.5–2.5× height of fruit body; annulus pubescent; stipules 2-lobed, lost early.

11a. Abaxial surface of leaves densely villous or tomentose over the entire surface; lateral veins (6)7 or 8(9) per side of blade midrib; petioles 6–12 mm; stipules retained through expansion of leaves, the lower lobe reniform; disc lobes lanceolate, acuminate, (1/3–)1/2 length of sepals; width of mericarps 12–15 mm, wings 6–7 mm high, seeds 2–2.2 mm long; Panama and Colombia ..... 3. *G. croatii*

11b. Abaxial surface of leaves with trichomes restricted to lateral vein axils (sometimes also present on venation); lateral veins 3 to 5 per side of blade midrib; petioles 10–25 mm; stipules lost before leaves expand, the lower lobe lanceolate or ovate; disc lobes transversely rectangular or square, 1/4–1/3(1/2) length of sepals; width of mericarps 14–20 mm, wings

(9–)10–14 mm high, seeds ca. 3.5 mm long; Mexico (Veracruz) to Honduras (Atlántida) ..... 10. *G. obamana*

10b. Fruit mericarps butterfly-shaped, the wings attached to apex and base of fruit body as well as sides, width across the entire mericarp 1.25–2× the height of the fruit body and distance between highest points of 2 wings of mericarp ≤ 1× height of fruit body; annulus pubescent or glabrous; stipules unlobed (or nearly so), or 2-lobed and usually retained.

12a. Stipules lost early, unlobed and lanceolate, acuminate (rarely with minute subulate foot); mericarps 6–9 mm wide, height of wings 4–6 mm, internal surface with fruit body drying dark red-brown, strongly contrasting with wings; Pacific Mexico ..... 13. *G. rosei*

12b. Stipules usually retained, with 2 lanceolate, acuminate lobes; mericarps 8–15 mm wide, height of wings 6–11 mm, internal surface with fruit body drying light brown, light gray-brown, or green-white, not or only slightly darker than wings; Yucatan Peninsula, Guatemala, Honduras, and Cuba.

13a. Leaves with lateral veins 7 or 8 per side of midrib; flowers and fruits drying dark ferruginous; width of fruit body 2/5 width of mericarp; 1500–2200 m elevation ..... 6. *G. ferruginea*

13b. Leaves with lateral veins 4 or 5(6) per side of midrib; flowers and fruits drying green and white, yellow-white, yellow-brown, or green-yellow; width of fruit body 1/4–1/3 width of mericarp; 0–520 m elevation.

14a. Annulus densely pubescent; mericarp fruit body 4–5 mm high, width of mericarp 8–9 mm; leaves frequently drying bicolored, abaxial surface drying green-white, totally covered between venation with tightly appressed trichomes to 0.1 mm long; Cuba; probably flowering in August ..... 4. *G. ekmanii*

14b. Annulus glabrous; mericarp fruit body (5)6–9 mm high, width of mericarp 11–15 mm; leaves not drying bicolored, the abaxial surface drying green, abundantly to sparsely pubescent (not totally covered between venation) with spreading trichomes 0.2–0.6 mm long; Yucatan Peninsula and Honduras; flowering generally in October and November (rarely through April) ..... 5. *G. eurycarpa*

1. Gouania colombiana Suess., Mitt. Bot. Staatssamml. München 1: 183. 1953. TYPE: Colombia. Meta: Sierra de la Macarena, Caño Entrada, 550 m, 30 Jan. 1950, *J. M. Idrobo 2357* (lectotype, designated here, M!; isolectotypes, BM!, US-2045210!, US-2844701!). Figures 1A, 2A.

Liana; young branches hollow in the center or solid, glabrous to densely and minutely puberulent, trichomes light red-brown. Leaf blades 9–18 × 5–14.2 cm, elliptic to widely elliptic or less frequently lanceolate to ovate, subcoriaceous, adaxial surface drying dark green-black, brown-green, brown (rarely yellow-green), rapidly glabrescent with trichomes retained only at apex, the trichomes 0.1–0.4 mm, straight, appressed and ascending, white, abaxial surface drying often slightly lighter than adaxial surface, dark green-black, brown, light brown, brown-green (rarely yellow-green), almost glabrous excluding trichomes dense at apex and sometimes sparse on veins, trichomes 0.05–0.25 mm, ± straight and appressed, white or red-brown, lateral veins (4)5(6) per side of midrib, diverging at 40°–60° angles, base cordate or subcordate, or less frequently rounded, margin serrulate, usually just apically or nearly entire, tooth glands truncate to cupular, apex acute then short-cuspidate, the margins of the cusp generally thickened; stipules unlobed (Fig. 1A), or often with a small broad foot, often retained through flowering, 1–2 × 1–2.5 mm, erect, appressed, ovate or reniform, acute or rounded, foot (if present) 0.25–0.5 × 0.25–1 mm, pointing downward, appressed, orbicular or ovate, rounded or acute; petioles 15–45 mm. Inflorescence with longest racemiform part 15–27 cm, rachis puberulent with trichomes yellow-white to ferruginous, bract of cyme ca. 1 mm, ovate, acute, cymes with peduncles 2–4.5 mm, mature flowers with pedicels 1.25–2.5 mm, hypanthium densely minutely sericeous or puberulent with trichomes white or yellow-white; sepals 0.7–1 mm, externally abundantly minutely sericeous or puberulent, trichomes white or yellow-white; petals 0.5–1 mm; stamens with filaments 0.5–0.6 mm, anthers 0.2–0.25 mm; disc excluding lobes 1–1.3 mm diam., glabrous, disc lobes 0.5–1 mm, lanceolate, acuminate, entire, 3/4–1× length of sepals; style glabrous. Young fruits sparsely puberulent, trichomes white; mature mericarps butterfly-shaped (Fig. 2A), the wings attached to apex and base of fruit body as well as sides, externally drying brown or yellow-brown, darker over fruit body, glabrous or with sparse, appressed trichomes at apex of fruit body (rarely over whole fruit body) to 0.1 mm, white, internally drying with wings yellow-brown, pale brown or white, with indistinct pale brown streaks, not or slightly contrasting with fruit body, same color as wings or very slightly darker, fruit body 6–10 mm high, wings 11–13 mm high, distance between highest points of 2 wings 5–6 mm, width of mericarp 10–17 mm, 1.2–2.2× height of fruit body, width of fruit body 2–3.2

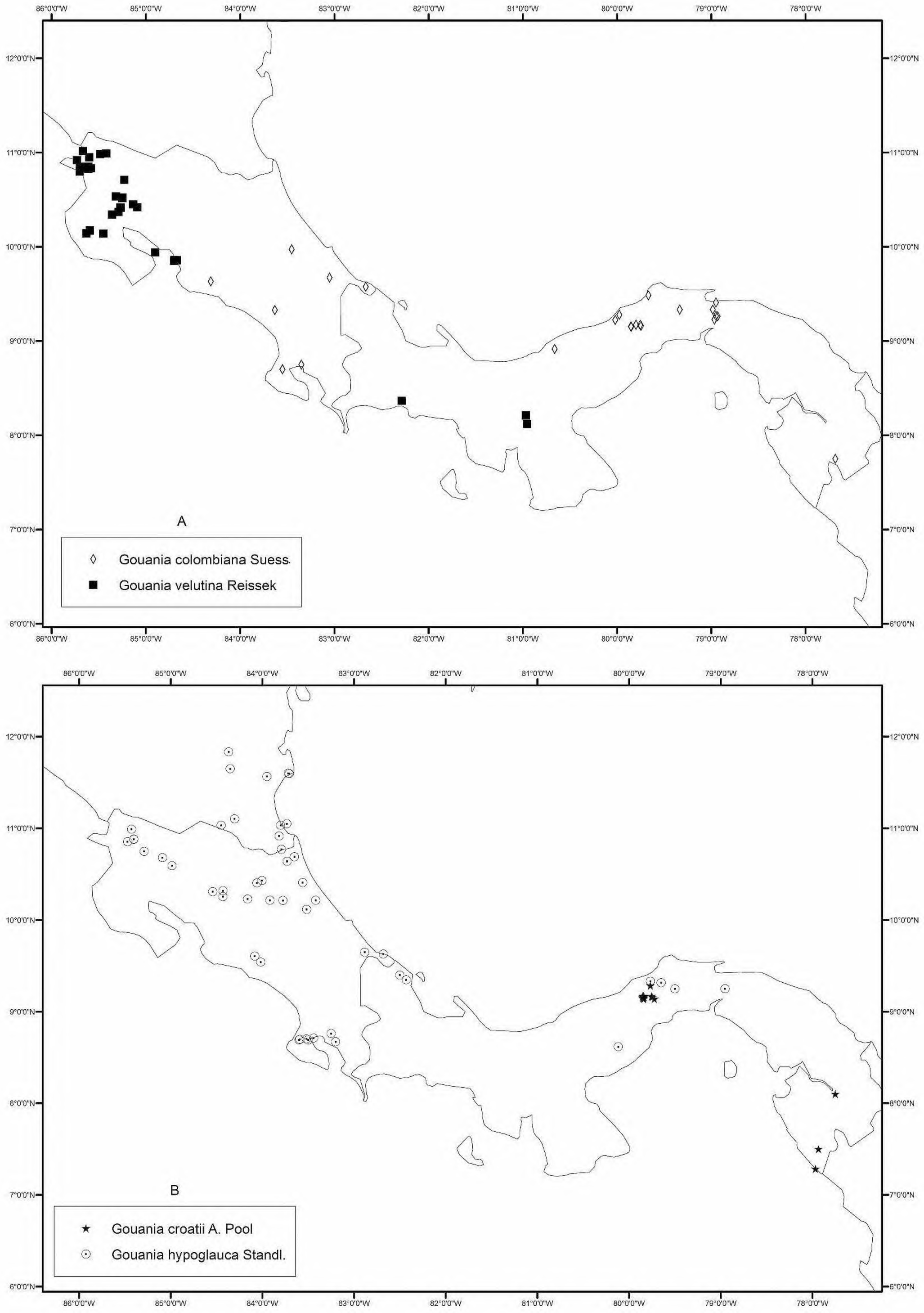


Figure 6. —A. Geographic distribution of *Gouania colombiana* Suess. in North America. Specimens of *G. colombiana* from South America are not mapped. Geographic distribution of *G. velutina* Reissek in Central America. See also the mapped distributions for *G. velutina* in Mexico (Fig. 5A) and in the Caribbean region (Fig. 8A). Specimens of *G. velutina* from South America are not mapped. —B. Geographic distribution of *G. croatii* A. Pool in North America. Specimens of *G. croatii* from northern South America are not mapped. Geographic distribution of *G. hypoglauca* Standl. across its known distributional range.

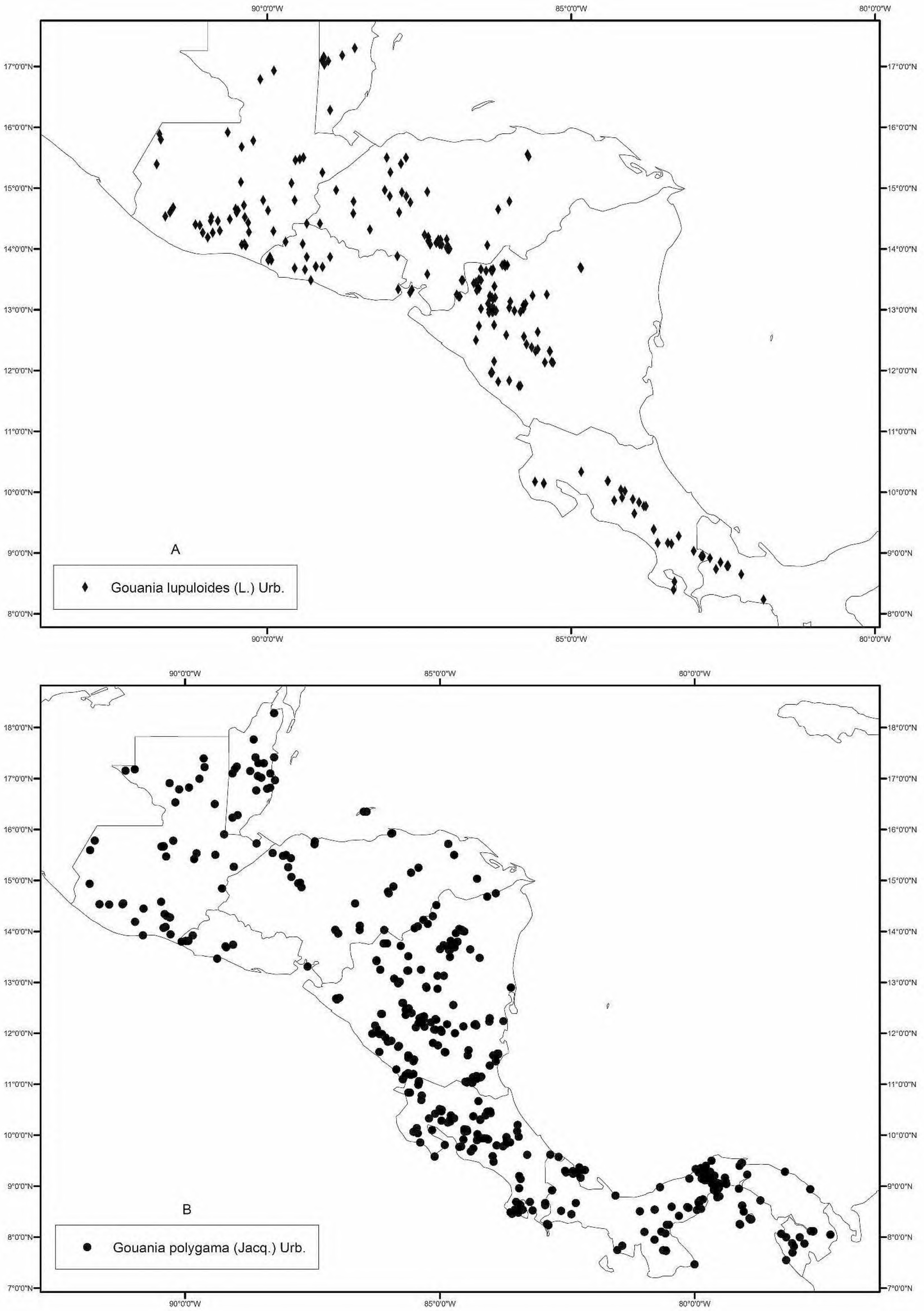


Figure 7. —A. Geographic distribution of *Gouania lupuloides* (L.) Urb. in Central America. See also the mapped distributions for *G. lupuloides* in Mexico (Fig. 3) and in the Caribbean region (Fig. 8A). —B. Geographic distribution of *G. polygama* (Jacq.) Urb. in Central America. See also the mapped distributions for *G. polygama* in Mexico (Fig. 4B) and in the Caribbean region (Fig. 8B). Specimens of *G. polygama* from South America are not mapped.

mm, 1/6–1/4 width of mericarp; seeds ca. 4 × 2 mm, light dull brown.

Habitat and distribution. *Gouania colombiana* is known from Costa Rica, Panama (Fig. 6A), Colombia, Ecuador, and Peru. It is found in wet and very wet forest, 0–600 m elevation, rarely to 1000 m in South America.

IUCN Red List category. This species is assessed as Data Deficient (DD), according to IUCN (2012) criteria. Based on its extent of occupancy, from Costa Rica through northwestern South America, *Gouania colombiana* would appear to be a species with least conservation concern. However, it is not at all common in Central America, with only 26 collections known to the author, and its conservation status requires further study.

Phenology. *Gouania colombiana* has been collected in flower in Central America in July and August (*Hammel et al. 18710*, with a few open flowers in January) and in South America from November to January, and rarely in July and March.

Discussion. Suessenguth (1953b) cited in the protologue of *Gouania colombiana* both the BM and M sheets of *J. M. Idrobo 2357*. Both sheets are annotated by Suessenguth and are of equally useful quality. The M sheet is chosen as the lectotype as it is at the home institution of Suessenguth and includes Suessenguth's drawing of the young fruit, which nicely illustrates the retained sepals and disc lobes.

Nowicke (1971) did not formally treat *Gouania colombiana* for Panama, but included a specimen citation, *Williams 723*, and a description of the same in her discussion below *G. lupuloides*, suggesting that it was a distinct species, but not identifiable from the material at hand. *Gouania colombiana* differs from *G. lupuloides* in its disc lobes (3/4–1× the length of the sepals and lanceolate, acuminate vs. usually 1/5–2/5 the length of the sepals and square to transversely rectangular), width of fruit body (2–3.2 mm, 1/6–1/4 the width of the mericarp vs. 3–5 mm, usually 1/4–1/2 the width of the mericarp), leaves usually glabrous excluding the tip and the tip with thickened margins versus leaf apices not more pubescent than rest of leaf nor with thickened margins, and stipules with upper lobe (or only lobe) ovate or reniform versus upper lobe lanceolate or triangular.

Croat (1978) treated a specimen of this species (*Foster s.n.* [Sep. 1969] from Barro Colorado Island, Panama) as *Gouania adenophora* Pilg. *Foster s.n.* [Sep. 1969] consists of two old mericarps found on the forest floor. One disc lobe is retained, and it is relatively long when compared to the retained sepal and is lanceolate and acuminate. The mericarps in all respects match those of other specimens of *G. colombiana*. The original description of *G. adenophora* is based on flowering material, and I do not know what fruiting specimens can be associated with this name. However, the disc lobes were described by Pilger (1915) as one half the length of the sepal lobes, with the apex truncate to retuse to truncate and then apiculate, different from the retained disc lobe of *Foster s.n.* [Sep. 1969]. Following Croat (1978), the name *G. adenophora* was frequently misapplied to specimens from Panama of *G. colombiana*. Nonetheless, *G. colombiana* is a distinctive species and rarely confused with other species. In addition to the disc lobe character, the type of *G. adenophora* (*E. Ule 16p*, B photo!) differs from *G. colombiana* in the leaves having six and seven lateral veins on either side of the midrib and the blade margins more markedly serrate and lacking apical thickening.

Additional specimens examined from Central America. COSTA RICA. **Cartago:** Turrialba, P. N. Barbilla, *Mora C. & Rojas 1410* (G, MO, NY). **Limón:** Limón, R. B. Hitoy Cerere, *Acosta et al. 2149* (MO), Talamanca, Cuena del Sixaola, *González et al. 1640* (MO; Fig. 1A). **Puntarenas:** Osa, R. F. Golfo Dulce, Rancho Quemado, *Hammel et al. 18508* (MO), *18710* (MO, TEX); Osa, R. F. Golfo Dulce, Serranías de Golfito, *Aguilar 5735* (G, MO); Parrita, cuenca del Pirrís-Damas, Barrio La Vasconia, *Rodríguez G. 7460* (MO). PANAMA. **Canal Area:** Pipeline rd., 5–7 mi. N of Gamboa, *Gentry 2047* (MO, US), *Gentry 3271* (MO); near Indio Tower, NW part of Canal Zone, *Johnston 1597* (A, MICH, MO); hills N of Frijoles, *Standley 27486* (US), *27595* (US); Barro Colorado Island, *Standley 31417* (US), near Armour 700 & Drayton 100 trails, *Foster s.n.* [Sep. 1969] (MO). **Colón:** Achiote, Ft. Clayton, *Tyson et al. 4519* (MO); trail S of Río Guanche, on ridge to Cerro Pan de Azúcar, *Mori & Kallunki 2005* (MO); Donoso Distr., site of proposed copper mine (MPSA), *McPherson & Merello 21204* (MO). **Darién:** around Caña, S Darién, *Williams 723* (NY, US). **Panamá:** headwaters of Río Chagres, Río Esperanza & Río Piedras, *de Nevers 4094* (MO); El Llano–Cartí rd., 9 mi. from Pan American Hwy., *Miller 852* (MEXU, MO, TEX); Chepo, N of El Llano, *Gentry 5572* (MO, TEX, US), Chepo, 5–6 mi. N of El Llano, near San Blas border, *Gentry 5795* (MO). **San Blas:** Nusagandi, El Llano–Cartí rd., *de Nevers & Todzia 3543* (MEXU, MO, TEX); El Llano–Cartí rd., 22–24.5 km from Interamerican Hwy., *de Nevers & Herrera 4269* (CAS, MO; Fig. 2A, NY, TEX, US).

Selected specimens examined from South America. COLOMBIA. **Antioquia:** Anorí, vía Dos Bocas-Providencia, *Callejas et al. 4555* (MO, TEX). ECUADOR. **Morona-**

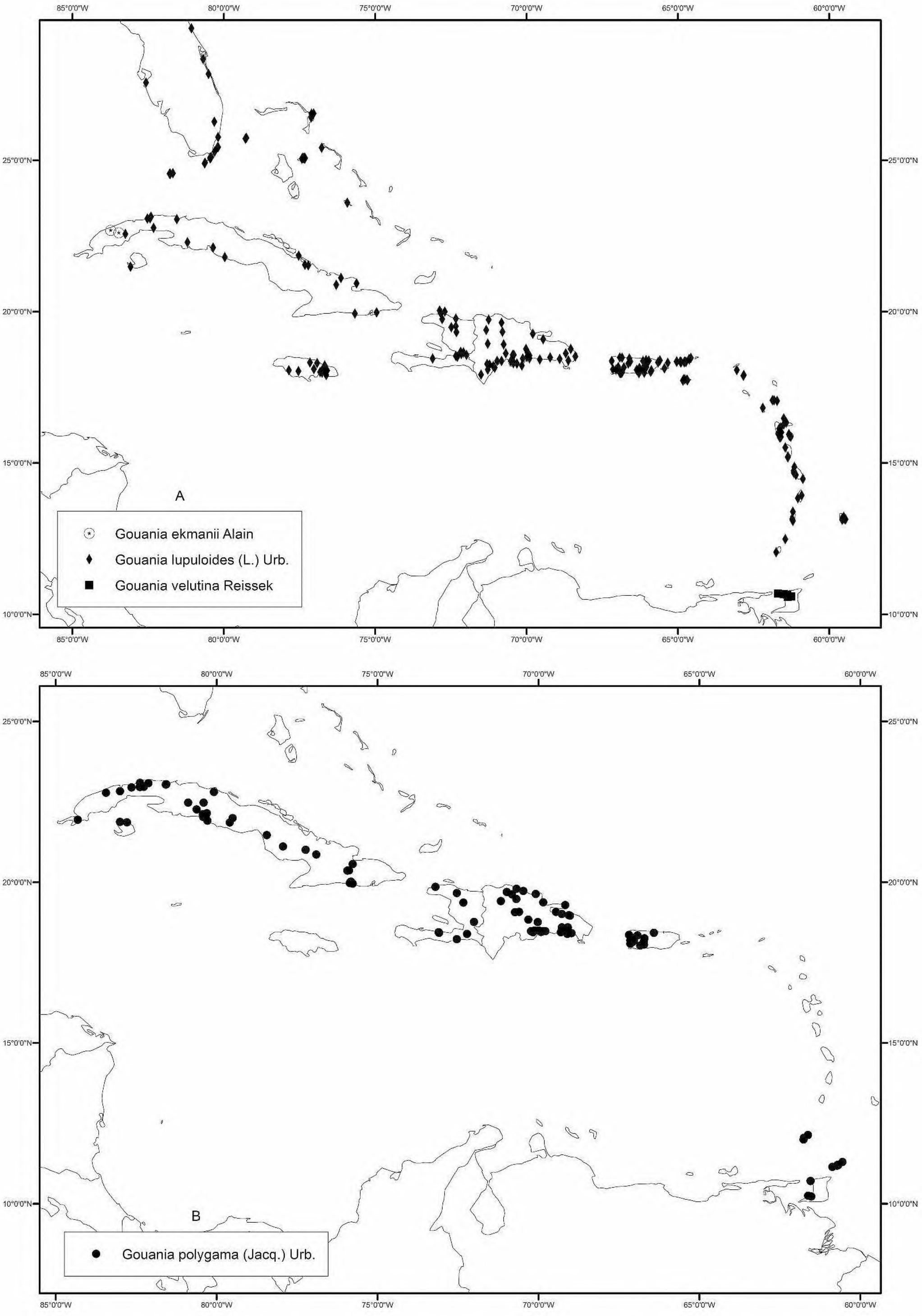


Figure 8. —A. Geographic distribution of *Gouania ekmanii* Alain across its known distributional range. Geographic distribution of *G. lupuloides* (L.) Urb. in Florida and the Caribbean region. See also the mapped distributions for *G. lupuloides* in Mexico (Fig. 3) and in Central America (Fig. 7A). Geographic distribution of *G. velutina* Reissek in the Caribbean region. See also the mapped distributions for *G. velutina* in Mexico (Fig. 5A) and in Central America (Fig. 6A). Specimens of *G. velutina* from South America are not mapped. —B. Geographic distribution of *G. polygama* (Jacq.) Urb. in the Caribbean region. See also the mapped distributions for *G. polygama* in Mexico (Fig. 4B) and in Central America (Fig. 7B). Specimens of *G. polygama* from South America are not mapped.

Santiago: 10 km O del Río Zamora y 2 k S del Río Bomboiza, *Baker 6836* (MO). **Napo:** Cantón Orellana, Sect. Huashito, 20 km N de Coca, prop. Palmoriente, *Rubio 328* (F, MO, TEX), *Gudiño 224* (MO, TEX); Aguarico, Chiro Isla community, N bank of Río Napo, *Bensman 298* (MO); vic. Tena, along rd. to Muyuna, *Croat 58834* (MO, TEX). **Orellana:** P. N. Yasuni, Km. 51 of Maxus Petroleum rd. (= YPF), near Río Natali, *Burnham & Krings 1571* (MICH, MO). **Pastaza:** 10 km al S del límite Napo-Pastaza, vía Auca ca. Río Tigüino, *Palacios 3469* (MO, TEX). PERU. **Amazonas:** Bagua, along rd. Chiriaco–Bagua, *van der Werff et al. 16352* (MO); Bagua, Yamayakat, *Jaramillo et al. 1362* (MO); Condorcanqui, Río Cenepa region, 10 km N of Huampami, *Berlin 861* (MO); Condorcanqui, Río Cenepa region, Quebrada Sasa, Monte, *Kayap 1237* (MO). **Loreto:** mouth of Río Santiago, *Tessmann 4682* (G); Maynas, Yanamono, Explorama Tourist Camp, *Gentry et al. 42963* (MO, TEX). **San Martín:** Rioja, Río Negro, Río Seco & Trapiche, *Woytkowski 6195* (G, MO, US). **Ucayali:** vic. of Aguaytía, *Mathias & Taylor 5019* (F).

2. Gouania conzattii Greenm., Publ. Field Columb. Mus., Bot. Ser. 2: 257. 1907. TYPE: Mexico. Oaxaca: Cerro San Felipe, 1700 m, 15 Sep. 1906, *C. Conzatti 1567* (holotype, F!). Figure 2B.

Liana; young branches solid, densely to sparsely pilose or tomentose, trichomes white to yellow, sometimes mixed with trichomes light red-brown to ferruginous or sometimes only ferruginous. Leaf blades 5–12.5 × 3.7–8 cm, elliptic to ovate, membranaceous, adaxial surface drying green, abundantly sericeous to tomentose (sometimes glabrescent) with trichomes 0.3–0.75 mm, white, abaxial surface drying similar green to adaxial surface to slightly paler, densely to sparsely tomentose with trichomes 0.3–0.75 mm, white, lateral veins (5)6 to 8 per side of midrib, diverging at 45°–70° angles, base subcordate or truncate and then shortly decurrent (rarely cordate), margin crenate to crenulate, 1 to 2 teeth/cm, tooth glands pulvinate (rarely cupular), apex acute or short-acuminate; stipules 2-lobed, often lost early, upper lobe 2–5 × 0.75–1.5 mm, erect, lanceolate, acuminate, lower lobe 1–2.5 × 0.25–1 mm, curving downward, lanceolate, acuminate (rarely linear); petioles 8–43 mm. Inflorescence with longest racemiform part 6–28 cm, rachis densely pilose (rarely tomentose) with trichomes white, white and ferruginous, or ferruginous, bract of cyme 1.75–4.5 mm, lanceolate, acuminate, cymes appearing sessile (rarely peduncle 3.5 mm), mature flowers appearing sessile to rarely pedicels to 1 mm, hypanthium densely villous with trichomes white; sepals 0.9–1.3 mm, externally densely villous, trichomes ferruginous or ferruginous and white; petals 0.75–1.25 mm; stamens with filaments (0.5)0.6–0.8 mm, anthers ca. 0.25 mm; disc excluding lobes 1.2–2 mm diam., glabrous or with few to numerous trichomes along annulus, disc lobes 0.25–0.35(0.5) × 0.35–0.8 mm at apex, square to transversely rectangular, generally apically bilobed, 1/4–1/3(1/2) length of sepals; style glabrous or pubescent at base. Young fruits glabrescent to pilose with trichomes sparse to scattered, ferruginous and white; mature mericarps butterfly-shaped (Fig. 2B), the wings attached to apex and base of fruit body as well as sides, externally drying light yellow-brown, darker brown over fruit body or yellow-green and darker green over fruit body, glabrous or fruit body apically with few appressed trichomes 0.05–0.1 mm, white or ferruginous, internally drying with wings white or yellow-white slightly or moderately contrasting with light to medium gray-brown fruit body, fruit body 5–6 mm high, wings 7–10 mm high, distance between highest points of 2 wings 7–10 mm, width of mericarp 12–15 mm, 2–3× height of fruit body, width of fruit body 4–5 mm, ca. 1/3 width of mericarp; seeds 3.5–3.75 × (2.5)2.75–3.1 mm, shiny brown.

Habitat and distribution. *Gouania conzattii* is known from Pacific to central Mexico, from Nayarit south to Oaxaca and east to México, Tlaxcala, and Puebla. The species is often found in oak forest, or associated with wooded ravines, between 1000 and 1700 (rarely to 2200) m elevations, with one collection (*McVaugh & Koelz 1092*, MICH) from 400 m (Fig. 3).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania conzattii* is a mid- to high-elevation species endemic to Mexico. It has a great extent of occupancy, but a relatively low estimated area of occupancy (132 km^2). With 57% of the collections falling outside of protected areas, this species is a candidate for further conservation study.

Phenology. *Gouania conzattii* has been collected in flower from May to October, with its peak from June to August.

Discussion. Standley (1923) suggested that *Gouania conzattii* might be better treated as a form of *G. polygama*. The two species are similar in often having the abaxial surface of the leaves densely pubescent (not always consistent in *G. polygama*) and the annulus of the flowers with trichomes (not always seen in *G. conzattii*). However, *G. polygama* has dumbbell-shaped mericarps and the floral disc lobes

are (1/3–)2/5–3/5(–2/3) the length of the sepals and often apically tapering. Specimens of *G. conzattii* are frequently misidentified as *G. polygama*, *G. lupoloides*, or *G. rosei*. *Gouania lupuloides* can be separated from *G. conzattii* following the key to species; *G. lupuloides* has leaves with usually fewer lateral veins per side (three to six), flowers always pedicellate, sepals and hypanthium drying concolorous, disc annulus always glabrous, and the mericarps of a slightly different shape, i.e., the distance between the highest points of the two wings of the mericarps of *G. lupuloides* 3–7 mm and (1/4–)1/3–1/2(–3/5) the width of the entire mericarp. *Gouania rosei* has mericarps densely pubescent and smaller (height of wings 4–6 mm, width of mericarp 6–9 mm), stipules unlobed or with lower lobe minute, and flowers without ferruginous trichomes. Standley and Steyermark (1949) included *G. conzattii* for Guatemala based on misidentified specimens of *G. lupuloides* (*Aguilar G. 219* and *Standley 61408*). In flower, *G. conzattii* is very similar to *G. ferruginea*, from Guatemala (see discussion under the latter species).

A probable hybrid between *Gouania lupuloides* and *G. polygama* from Chiapas has been observed, which might be confused with *G. conzattii*. It has, in common with *G. conzattii*, six or seven pairs of lateral leaf veins, disc lobes transversely rectangular and 1/3 the length of the sepals, and annulus with trichomes, but differs in the sericeous, yellow-white trichomes on the sepals and hypanthium. For further detail, see discussion under *G. polygama*.

Additional specimens examined. MEXICO. **Colima:** above Río Salado, 5 mi. S of Colima, *McVaugh & Koelz 1092* (MICH); Comala, Rancho El Jabali, ca. 22 km NNW of city of Colima, *Sanders et al. 8586* (TEX), 22 km (airline) NNW of Colima in SW foothills of Volcán de Colima, *Sanders et al. 10886* (MEXU, TEX), *Vázquez V. & Phillips 820* (MEXU, TEX), *Vázquez V. 1610* (MICH), *Vázquez V. & Phillips 911* (MEXU), *Vázquez V. & Phillips 604* (MEXU, TEX), 22 km NNW of city of Colima, near Epazote, *Sanders et al. 8335* (TEX), 20 km (airline) N of Colima in SW foothills of Volcán de Colima, *Sanders et al. 11778* (MICH, TEX); Cuauhtemoc, 3 km al NE de Quesería, límite de Colima–Jalisco, *Santana M. & Cervantes A. 1062* (MEXU). **Guerrero:** Manchón, *Hinton 9615* (K, LL, US). **Jalisco:** Mpio. Zapotitlán, Volcán de Colima, Rancho El Jabalí, 20 km (airline) N of Colima, in the SW foothills of the Volcán de Colima, *Sanders et al. 11843* (MICH, TEX); Agua Fría, brecha a Manuel M. Dieguez, Tamazula, *Díaz L. 3620* (MICH, TEX); Zapotlán, *Ross 456* (M); Acatlán de Juárez, el arroyo Colorado, *Machuca N. 6596* (MICH, TEX); Sierra Madre Occidentale, San Gerónimo, rd. to Quila, *Provance 8166* (MO); Tala, vic. de Ahuisculco, *Machuca N. 7710* (MEXU); Tamazula de Cordiano, Hwy. 110, vic. of Tamazula, *Croat 45467* (MEXU, MO; Fig. 2B); E de Tecalitlán, brecha a Jilotlán, *Villa C. 347* (MICH), *Villa C. et al. 872* (MICH); 13.4 km N de Venustiano Carranza, camino a Tapalpa, *Lott & Solís M. 775* (MEXU, TEX); Mpio. Venustiana Carranza, brecha Venustiana Carranza a Tapalpa, *Vigueras G. et al. 60* (MICH); Mpio. Venustiana Carranza, camino a Rancho de los Ramírez, *Martínez 512* (MEXU); Zapotitlán de Vadillo, Rancho El Jabalí, *Vázquez V. 1462* (MICH, MO). **México:** Temascaltepec, Villaneda, *Hinton 6531* (LL, MICH, NY). **Nayarit:** Arroyo de la Fundición, 5 mi. SE of Ahuacatlán, *McVaugh 16357* (MICH); Ahuacatlán, mtns. 10 mi. SE of Ahuacatlán, *Feddema 331* (MICH). **Oaxaca:** Hac. Guadalupe, 9 June 1907, *Conzatti s.n.* [9 June 1907] (LL, NY); Guadalupe, *Conzatti 1829* (MEXU); valley of Oaxaca, *Nelson 1524* (US); San Lorenzo Albarradas, *Torres B. 2297* (MEXU), *2423* (MEXU); 9 km al NE Teotitlán del camino, rumbo a Huautla, *González M. et al. 1460* (MO); 19 km by rd. NE of Mitla, *Webster & Armbruster 21075* (MEXU, TEX); 18 mi. NE of Sola de Vega, *Webster et al. 13056* (MEXU, MO); Mpio. Tepelmeme, Cañada de Carrizalillo, Cerro Verde, *Tenorio L. et al. 6959* (TEX); Centro, hac. Guadalupe, *Conzatti 4902* (MEXU); Mpio. Telixtlahuaca, Etla, "Parian-Las Sedas," *Salinas T. et al. 6865* (MO); Juxtlahuaca, Río Mixtepec, *Reyes S. 1670* (MEXU); Juxtlahuaca, a 10 km al NO de San Juan Mixtepec, *Reyes S. 2072-A* (F); Nochixtlan, El Parian, *Conzatti 1935* (F); 2.5 km al SO del centro de San Andrés Huayapam, *Carrillo-Reyes 5546* (MO). **Puebla:** Río de Santa Lucía, vic. San Luis Tultitlanapa, *Purpus 3172* (F, GH, MO, NY); Coxcatlán, *Purpus 4198* (F, MO, NY). **Tlaxcala:** Barranca de Tlacuilosto, *Purpus 6498* (G, M).

3. Gouania croatii A. Pool, sp. nov. TYPE: Panama. Darién: Río Jaqué, disturbed tropical wet forest on flat river flood plain, 7°27′N, 78°05′W, 100 m, 29 Jan. 1982, *S. Knapp & J. Mallet 3218* (holotype, MO!; isotypes, TEX!, PMA not seen). Figures 2C, 9A–E.

Diagnosis. New species similar to *Gouania polygama* (Jacq.) Urb. but with pubescent mericarps and the lower lobe of the stipule foliaceous and reniform.

Liana; young branches solid, densely villous or velutinous, trichomes ferruginous to light red-brown. Leaf blades 6–12 × 3–9 cm, widely elliptic, membranaceous, adaxial surface drying dark red-brown (less frequently dark green), moderately to densely sericeous to pilose with trichomes 0.3–1 mm, white to light red-brown, abaxial surface drying yellow-green, densely villous or tomentose with trichomes 0.5–1 mm, spreading and matted, white or tawny or with reddish tint on lateral veins, lateral veins (6)7 or 8(9) per side of midrib, diverging at 25°–45° angles, base narrowed then cordate and finally short-decurrent or narrowed then truncate, margin crenate or crenulate, 0.5 to 2 teeth/cm, tooth glands pustular to cupular at maturity, apex obtuse and apiculate (rarely obtuse and cuspidate); stipules 2-lobed, caducous or retained in part, upper lobe 4.5–7 × 1.5–2.5 mm, spreading upward, lanceolate, often asymmetrically so, acuminate, lower lobe 2.5–4 × 3–5 mm, spreading downward, foliaceous, reniform, frequently strongly concave, the margins strongly

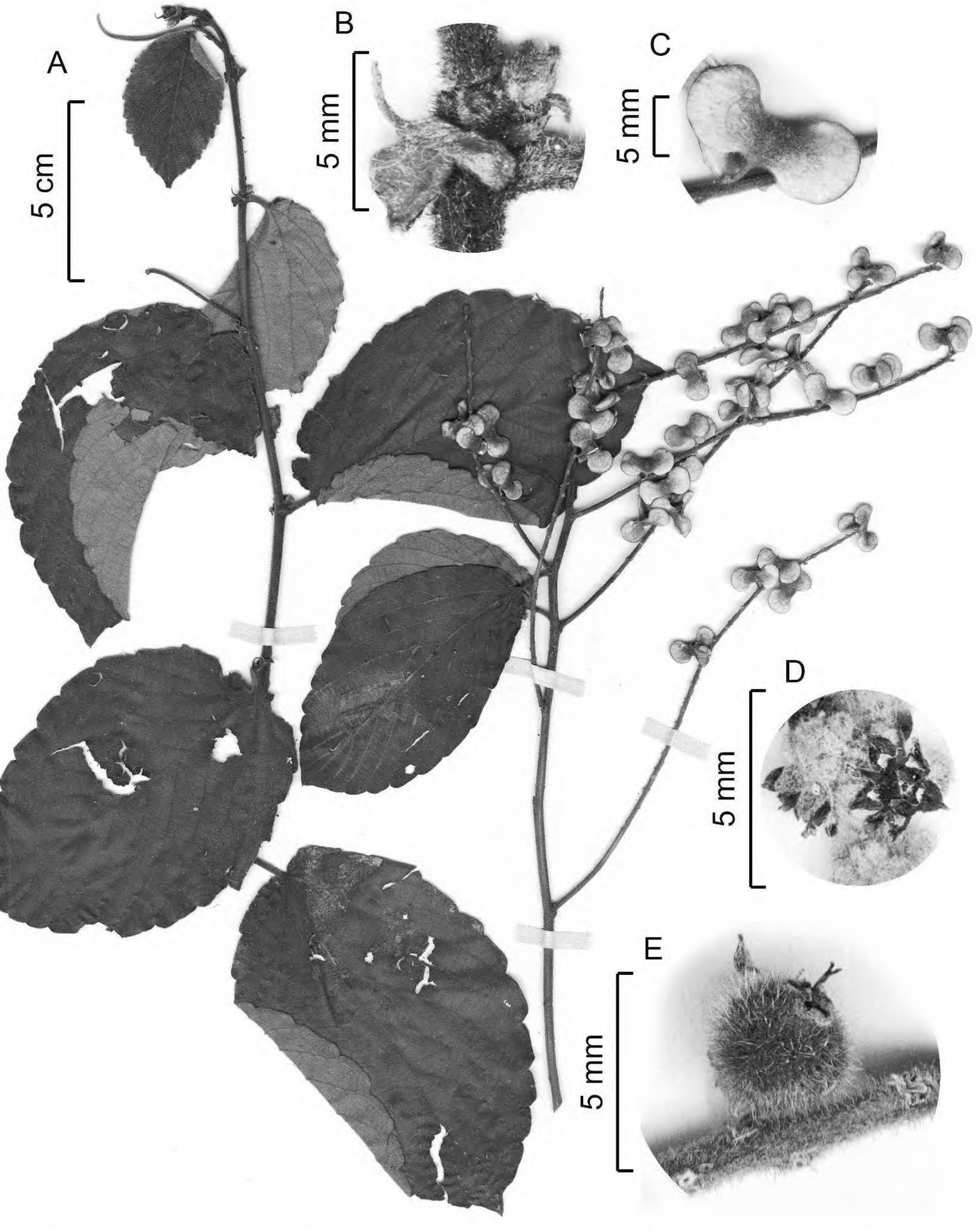


Figure 9. *Gouania croatii* A. Pool. —A. Two branches, one vegetative and one fruiting. —B. Stem node with stipule. —C. Fruit. —D. Flower at inflorescence node. —E. Young fruit. A–C scanned from the holotype *S. Knapp & J. Mallet 3218* (MO); D scanned from the paratype *R. J. Schmalzel & T. M. Aide 106* (MO); and E scanned from the paratype *T. B. Croat 7274* (MO).

curving inward, rounded or rarely with extended caudate tip; petioles 6–12 mm. Inflorescence with longest racemiform part 11–15 cm, indumentum of rachis similar to that of young branches, bract of cyme 2.25–3 mm, narrowly lanceolate, acuminate with a long extended tip, the cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.5 mm, hypanthium and sepals externally densely sericeous with trichomes yellow-white, or occasionally also with scattered ferruginous trichomes; sepals 0.75–1 mm; petals 0.5–0.8 mm; stamens with filaments 0.4–0.8 mm, anthers 0.15–0.25 mm; disc excluding lobes 1–1.4 mm diam., annulus with few to numerous trichomes, disc otherwise glabrous, disc

lobes 0.3–0.5 mm, generally lanceolate, acuminate (or with some to 0.2 mm wide at apex), apically entire or bilobed, (1/3–)1/2 length of sepals; style pubescent at base. Young fruits densely velutinous, trichomes ferruginous or light red-brown; mature mericarps dumbbell-shaped (Fig. 2C), the wings ± attaching to the sides of fruit body only, externally drying white-yellow, but surface in part obscured by indumentum, densely velutinous over fruit body and abundantly villous on wings with trichomes 0.3–0.6 mm, ferruginous, internally drying with wings yellow-white and fruit body slightly darker with faint brown rays extending into wings, fruit body 3–4 mm high, wings 6–7 mm high, distance between highest points of 2 wings 8–10 mm, width of mericarp 12–15 mm, 3–3.5 × height of fruit body, width of fruit body 2–3 mm, 1/6–1/4 width of mericarp; seeds 2–2.2 × 1.5–1.75 mm, green-brown to brown.

Habitat and distribution. *Gouania croatii* is known from Panama, from the Canal Zone area, Colón and Darién (Fig. 6B), and Chocó, Colombia. It is found in wet disturbed forests, 0–100 m in elevation. Some specimen labels indicate collection in river flood plains (e.g., *S. Knapp & J. Mallet 3218*, *Whitefoord & Eddy 209*). Many of the collections were made on Barro Colorado Island, all except *Shattuck 523* in coves with high silt deposits (Croat, 1978).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) critieria, *Gouania croatii* is known from only 19 collections in Panama and Colombia. However, as this study concentrated on the North American species of the genus, it is possible that this species may be more common in northern South America. Assignment of conservation status should await further study.

Phenology. *Gouania croatii* has been collected in flower in November and December.

Etymology. The new species is named for Thomas Bernard Croat, MO curator (1938–), who suggested (Croat, 1978) that this entity might (with further study) be worthy of specific or varietal recognition.

Discussion. *Gouania croatii* is most similar to *G. polygama*, a species known from Mexico to South America and the West Indies. *Gouania croatii* differs from *G. polygama* by its pubescent mericarps (vs. nearly glabrous in *G. polygama*) and its stipules, the lower lobes of which are foliaceous and reniform versus the stipule lobes small and acute to acuminate or rarely oblong or subulate. They are difficult to separate in flower, as the stipules of both species tend to be lost early; *G. croatii* is in general more densely pubescent than *G. polygama*. Perhaps also of interest is the occurrence of *G. croatii* in areas with high silt accumulations. On Barro Colorado Island, all but one collection were made in coves with high silt accumulation, while specimens of *G. polygama* were found inland or on points. Nowicke (1971) treated *G. polygama* as a synonym of *G. lupuloides* (see discussion of *G. polygama* below), and cited the following specimens from Panama of the species here published as *G. croatii* under *G. lupuloides*: *Croat 7984*, *Shattuck 444*, and *Woodworth & Vestal 326*. Croat (1978) also treated *G. polygama* as a synonym of *G. lupuloides*, but suggested that two forms of the species were present on Barro Colorado Island, which, under further monographic study, might warrant varietal or specific recognition, and cited specimens for the form that he recognized as less common and more pubescent (*Croat 7274*, *7984*, *12699*, *12739*, *13482*; *Shattuck 290*, *444*, *523*; and *Woodworth & Vestal 326*). These represent the species described here and named in honor of Thomas Bernard Croat. Specimens from Colombia (Antioquia, Bolívar, Boyacá, Chocó), Venezuela (Falcón), Ecuador (Esmeraldas and Napo), and Peru (Amazonas) that are similar to *G. croatii* but with different stipules (upper lobe lanceolate and acuminate, lower lobe linear to subulate; e.g., *E. Forero et al. 5188*, MO, and *R. Vásquez et al. 18574*, MO) and different coloration pattern on the internal surface of the mericarp (drying light brown over the fruit body with well-developed brown rays extending into the wings, e.g., *E. Forero et al. 4173*, MO, and *W. Palacios 2449*, MO) are kept separate from *G. croatii*, pending further study.

Paratypes. PANAMA. **Canal Area:** Pipeline rd., 5–10 mi. N of Gamboa, *A. H. Gentry 2650* (GH, MICH, MO); Pipeline rd., 8 km NW of Gamboa, *M. Nee 8432* (GH, MO); Pipeline rd., 2.3 mi. from gate, *T. B. Croat 12739* (MO, NY); Barro Colorado Island, *O. E. Shattuck 290* (MO), *444* (MO), Zetek Trail, marker 247, *O. E. Shattuck 523* (F, MO), cove N of laboratory, *R. H. Woodworth & P. A. Vestal 326* (MO), Hydrilla Cove, *R. J. Schmalzel & T. M. Aide 106* (MEXU, MO, TEX), Fuertes Cove, *T. B. Croat 12699* (MO, NY), shoreline of cove N of dock, *T. B. Croat 7274* (F, MO, NY), shoreline S of large cove N of Burrunga Point, *T. B. Croat 7984* (MO), shoreline of large cove S of Orchid Island, *T. B. Croat 13482* (F, MO; Fig. 2C). **Colón:** Gatún, *S. Hayes 122* (NY). **Darién:** Río Cocalito, *C. Whitefoord & A. Eddy 209* (BM, MO); rd. betw. El Real & Pijibasal, *R. L. Hartman 12015* (MEXU, MO, TEX).

COLOMBIA. **Chocó:** Mpio. Riosucio, zona de Urabá, cerros del Cuchillo, sect. Cuchillo Negro, orilla quebrada Cedros, *D. Cárdenas 1174* (MO), sect. Cuchillo Blanco, *D. Cárdenas 2054* (MO).

4. Gouania ekmanii Alain, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 12: 5. 1953. TYPE: Cuba. Pinar del Río: Mogote de la Baliza, Sra. de las Guacamayas, 8 Nov. 1923 [10 Aug. 1923, in protologue], *E. L. Ekman 17985* [*17895*, in protologue] (holotype, HAC [transfer from LS], HAC photo!, digital image!; isotypes, A!, F [packet only]!, NY [packet only]!). Figure 2D.

Liana; young branches solid, densely pilose, trichomes white to light red-brown. Leaf blades 4–5.5 × 2–2.8 cm, oblong, membranaceous to subcoriaceous, adaxial surface drying gray-green to dark green, scattered to densely puberulent with trichomes 0.05–0.1 mm, at right angles to surface, white, abaxial surface green-white, surface between venation totally covered with trichomes 0.05–0.1 mm, trichomes on venation to 0.25 mm, all trichomes straight, appressed and white, lateral veins 5 or 6 per side of midrib, diverging at ca. 60° angles, base cordate, margin serrate to serrulate, 2 to 4 teeth/cm, tooth glands pustular, apex obtuse to acute; stipules 2-lobed, at least some retained into young fruit, upper lobe 2.5–3.25 × 0.75–1.5 mm, erect, lanceolate, acuminate to long extended, flexuous tip, lower lobe 0.75–1 × 0.5 mm, curving downward, lanceolate, acuminate; petioles 5–13 mm. Inflorescence with longest racemiform part ca. 1 cm, rachis velutinous with trichomes white, bract of cyme ca. 2.25 mm, lanceolate, acuminate, cymes appearing sessile, mature flowers with pedicels ca. 1.25 mm, hypanthium and sepals externally densely velutinous with trichomes yellow-white; sepals ca. 0.75 mm; petals ca. 0.75 mm; stamens with filaments ca. 0.3 mm, anthers ca. 0.3 mm; disc excluding lobes ca. 1.25 mm diam., annulus with numerous trichomes, disc otherwise glabrous, disc lobes ca. 0.25 × 0.7 mm at apex, transversely rectangular, apically bilobed, 1/3 length of sepals; style glabrous. Young fruits not observed; mature mericarps butterfly-shaped (Fig. 2D), the wings attached to apex and base of fruit body as well as sides, externally drying with green to white wings and green fruit body, densely velutinous with trichomes 0.05–0.25 mm, white, internally drying with wings and fruit body a similar green-white, fruit body 4–5 mm high, wings ca. 6 mm high, distance between highest points of 2 wings 5–6 mm, width of mericarp 8–9 mm, ca. 2× height of fruit body, width of fruit body 2.75–3 mm, 1/4–1/3 width of mericarp; seeds 2.3–2.75 × 1.7–1.75 mm, shiny brown.

Iconography. Liogier (1953a: 6, fig. 6).

Habitat and distribution. *Gouania ekmanii* is endemic to the hills of Pinar del Río Province, Cuba. It has been collected on limestone and from 290 to 500 m in elevation (Fig. 8A).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania ekmanii* is known from only four collections from Pinar del Río Province, Cuba. Further study is urged to determine if it is endangered or critically endangered.

Phenology. Only one flowering collection of *Gouania ekmanii* is known. The date on the label is 8 November 1923, but there is reason to question this (see discussion below).

Discussion. Liogier (1953a) cited the type of *Gouania ekmanii* as *Ekman 17895*, collected 10 Aug. 1923, with the holotype deposited at LS and an isotype at NY. Figure 6 (Liogier, 1953a: 6) was published as a photo of the holotype. The specimen described and depicted is in fruit. The LS herbarium was transferred to HAC, and I received from HAC a scanned image of the holotype, the fruiting specimen pictured in figure 6 of Liogier. The collection number of this specimen is *17985* (not *17895*) and the date is 8 Nov. 1923 (not 10 Aug. 1923). The specimen at A has the same collection number and date as the holotype and is clearly an isotype. The NY specimen of *E. L. Ekman 17985* has two labels, one on the sheet, dated 10 Aug. 1923, and another on the packet, dated 8 Nov. 1923; the material both on the sheet and in the packet is in fruit. The F sheet of *Ekman 17985* is in flower and has a label with the collection date 8 Nov. 1923; fruiting material is in a packet. The isotypes of *G. ekmanii* at F and NY are the specimens in the packets only. The flowering material was probably not collected at the same time as the fruiting material. It is likely that the original flowering collection was actually made on 10 Aug. 1923 and the fruiting collections on 8 Nov. 1923, and the labels misapplied. If this is correct, then the sheet at NY would also be an isotype.

Gouania ekmanii is most similar when in fruit to *G. eurycarpa*, but can be easily separated using the key to species; *G. eurycarpa* with the disc annulus glabrous, fruit body usually 6–9 mm high, mericarp 11–15 mm wide and the abaxial surface of the leaves with trichomes spreading, 0.2–0.6 mm long and not totally covering the surface. Specimens of *G. ekmanii* were identified by Urban as *G. polygama*, which has a different leaf pubescence, mericarps nearly glabrous and dumbbell-shaped, and flowers with the disc lobes often apically tapering and usually longer relative to sepals, (1/3–)2/5–3/5(–2/3). *Gouania hypoglauca* has leaf pubescence similar to that of

G. ekmanii but usually has fewer lateral veins (three or four) on either side of the blade midrib, the entire nonlobed part of the flowering disc pubescent, and larger mericarps (height of wings 9–14 mm, width of mericarp 10–15.3[17] mm).

Additional specimens examined. CUBA. **Pinar del Río:** Sierra del Ancón, Viñales, *Liogier 6862* (PR; Fig. 2D); Mogote de la Baliza, Sra. de las Guacamayas, *Ekman 17985* (NY); Sierra del Sitio Santo Tomas, Ensenada de Vega Cuchilla, *Ekman 16675* (BM, F).

5. Gouania eurycarpa Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 315. 1929. TYPE: Honduras. Yoro: near Progreso, 30 m, 24 Jan. 1928, *P. C. Standley 54988* (holotype, F!; isotypes, A!, G fragm.!, US!). Figure 2E.

Liana; young branches generally hollow, densely to abundantly villous to pilose, trichomes white or light red-brown. Leaf blades 5–10.5 × 2.5–6.7 cm, elliptic or less frequently ovate, membranaceous, adaxial surface drying green, abundantly pubescent to glabrescent with trichomes 0.25–0.5 mm, appressed, ascending, straight to slightly curved, white to light red-brown, abaxial surface drying similar green to adaxial surface to slightly paler, abundantly to sparsely pubescent with trichomes 0.2–0.6 mm, spreading in all directions, straight or slightly curved, white or light red-brown, lateral veins 4 or 5(6) per side of midrib, diverging at 45°–75° angles, base generally subcordate to rounded (rarely cordate), margin serrate to serrulate (rarely crenate or crenulate), 1 to 2 teeth/cm, tooth glands pulvinate to cupular, apex acute to acuminate; stipules 2-lobed, usually retained through fruiting, upper lobe 3–6.5 × 0.75–1.5 mm, flexuous, lanceolate, acuminate, lower lobe 1–3.5 × 0.35–1 mm, spreading then curving up and/or down, lanceolate (rarely linear), acuminate; petioles 4–13(18) mm. Inflorescence with longest racemiform part 6.5–15 cm, indumentum of rachis similar to that of young branches, bract of cyme 2–5 mm, narrowly lanceolate to nearly linear, acuminate, cymes appearing sessile to peduncle 1 mm, mature flowers with pedicels 0.75–2 mm, hypanthium densely velutinous with trichomes yellow-white or sometimes mixed with light red-brown; sepals 0.75–1.2 mm, externally densely sericeous, trichomes yellow-white or mixed with light red-brown; petals 0.65–1.1 mm; stamens with filaments 0.5–1 mm, anthers 0.2–0.25 mm; disc excluding lobes 0.9–1.6(2) mm diam., glabrous, disc lobes 0.2–0.4 × 0.2–0.5 mm at apex, square to transversely rectangular, generally apically bilobed, 1/4–1/3 length of sepals; style glabrous. Young fruit densely velutinous, trichomes white to yellow or light red-brown; mature mericarps butterfly-shaped (Fig. 2E), the wings attached to apex and base of fruit body as well as sides, externally drying yellow-brown or green-yellow on wings and fruit body darker brown or brown-green, densely velutinous over fruit body to scattered pilose on wings with trichomes 0.2–1 mm, white and light red-brown, internally drying with wings yellow-white contrasting slightly with light gray-brown fruit body, fruit body (5)6–9 mm high, wings (6)8–11 mm high, distance between highest points of 2 wings 5–8 mm, width of mericarp 11–15 mm, 1.5–2× height of fruit body, width of fruit body 3–4 mm, 1/4–1/3 width of mericarp; seeds 3–3.75 × 2.2–2.75 mm, shiny brown.

Iconography. Krings and Braham (2005: 126, tab. 10.1, fig. C, c as *Gouania lupuloides*).

Distribution. *Gouania eurycarpa* is known from the Yucatan Peninsula (Belize, Guatemala [Petén], and Mexico [Campeche, Yucatán, Quintana Roo, and the border of Chiapas and Petén]) and the type from Atlantic Honduras. Collections are noted from sub-deciduous to sub-evergreen forest and from 0 to 520 m in elevation (Figs. 3, 5B).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania eurycarpa* is endemic to relatively wet forests of the Yucatan Peninsula and Atlantic Honduras where it is known from 109 collections and has an estimated area of occupancy of 312 km². Studies should be conducted to determine what is restricting its distribution and what risks the species faces before determining its conservation status.

Phenology. *Gouania eurycarpa* has generally been collected in flower in October and November and, rarely, from December through April.

Discussion. *Gouania eurycarpa* is most similar to *G. ferruginea*, but the latter species is restricted to upper elevations (1500–2200 m) in the mountains of Guatemala and Honduras. The two species can be separated following the key to species (for further discussion see *G. ferruginea*). The specimen cited for Guatemala by Standley and Steyermark (1949) as *G. eurycarpa* (*Standley 59894*) is a fruiting collection of *G. ferruginea*, and no herbarium collections of true *G. eurycarpa* from Guatemala were known at the time of that publication. Without fruit, *G. eurycarpa* is very difficult to separate from the widespread and very variable *G. lupuloides*. However, even in very young fruit they can be separated by the sparsely pilose or sericeous fruits of *G. lupuloides* versus the densely velutinous fruits of *G. eurycarpa*, and in flower the

indumentum of the hypanthium of *G. lupuloides* is sericeous versus velutinous in *G. eurycarpa*. In addition, while abaxial leaf pubescence is variable in *G. lupuloides* throughout its geographic range, in the Yucatan Peninsula (where *G. eurycarpa* is primarily found) the trichomes of the actual surface (vs. those on the venation) are straight, appressed and ascending versus spreading in all directions in *G. eurycarpa*. In the Mexican states of the Yucatan Peninsula, the two species form an interesting distribution pattern, with *G. lupuloides* found toward the Gulf of Mexico side and *G. eurycarpa* on the Caribbean side. *Gouania eurycarpa* was not recognized in Balick et al. (2000) for Belize, but specimens of *G. eurycarpa* are cited under both species of *Gouania* that they do recognize, *G. lupuloides* (*Arvigo & Cocom 703*, *Balick et al. 2121*, and *Gentle 236*) and *G. polygama* (*Gentle 1081* and *Warrior 2325*). *Gouania polygama* is most easily separated from *G. eurycarpa* by its dumbbell-shaped, nearly glabrous mericarps and flowers with a ring of trichomes around the disc annulus. Occasionally, specimens of *G. eurycarpa* are misidentified as *G. rosei* (Pacific Mexico), but these can be easily separated using the key to species; *G. rosei* with smaller mericarps (6–9 mm wide, height of wings 4–6 mm), fruit body drying dark red-brown on internal surface, and the stipules caducous and unlobed. The name *G. eurycarpa* has often been misapplied to Costa Rican specimens of *G. velutina*, and the illustration in Krings and Braham (2005) labeled as *G. eurycarpa* (tab. 10.1, fig. A) and the voucher cited thereunder (*Berrocal & Sánchez 107*, MO) actually correspond to *G. velutina*; see discussion under *G. velutina*.

Selected specimens examined. BELIZE. s. loc., *Warrior 2325* (NY). **Cayo:** Caracol Maya Ruins, 14 km W of Las Cuevas, *Hawkins 1156* (MO); Chaa Creek, *Arvigo & Cocom 703* (GH, NY, TEX). **Corozal:** s. loc., *Gentle 236* (A, F, MICH, NY, US); San Andrés, *Gentle 1081* (A, F, K, MICH, MO, NY); Ranchito, *Balick et al. 2121* (GH, MO, NY, US). **Orange Walk:** Rio Bravo Conserv. & Managem. Area, *Brokaw & Schulze 194* (BM, MO). GUATEMALA. **Petén:** Tikal Nat. Park, Tikal, Temple V, *Lundell 15396* (DS, F, LL, NY), bordering airfield, *Lundell 15321* (CAS, F, LL), Group H, on top of temple, *Contreras 368* (DS, LL, MO), Tikal, *Cantrall 2* (MICH), camino para el Remate, Km. 59, *Tún Ortíz 447* (F, MO, NY); Lago Petén Itzá, der Strasse von San José nach Nuevo San José, *Wallnöfer 9483* (MO, MSB, NY); Lago Petén Itzá, 0.3 km W der Strasse von San José nach Nuevo San José, *Wallnöfer 9540* (K, MO, MSB, NY). MEXICO. **Campeche:** Tuxpeña, *Lundell 1030* (F, GH, MICH, MO, NY); Calakmul, a 0.8 km al O de la Zona Arqueol. Nadzcaan, *Álvarez & Abascal 2838* (MEXU); Calakmul, 34 km al S de la caseta de entrada a Calakmul, *Martínez S. et al. 29963* (MEXU, MO); Calakmul, 3 km al W de Eugenio Echeverria Castellot I, *Martínez S. et al. 29593* (MEXU, MO, TEX); Calakmul, 3 km al E de Ley de Fomento, *Martínez S. et al. 30105* (MEXU, MO); Calakmul, 2 km al SE de Dos Naciones, *Martínez S. et al. 29275* (MEXU, MO, TEX); Escárcega, 98 km E of Francisco, *Johnson & Conway 406-78* (MO); Hopelchén, 12 km al NW de Ucum, *Martínez S. et al. 29762* (MEXU); Hopelchén, al S de Xpujil, *Chan V. 4573* (MO; Fig. 2E). **Chiapas:** Ocosingo, 14 km al NW de Crucero Corozal, sobre el Camino Palenque Boca Lacantum, *Martínez S. 16674* (F, GH, MEXU, MO). **Quintana Roo:** 5 km beyond Valladolid Nueva, toward Puerto Juarez, *Schubert & Gómez Pompa 1632* (A, MEXU); en los alrededores de la Laguna Muyil, 20 km S de Tulum, *Cabrera C. & de Cabrera 3969* (MEXU, MO); en la brecha al antiguo aereopuerto de Cancún, *Cabrera C. & Ibarra Manríquez 1443* (BM, MEXU); Puerto Morelos, 2 km al N camino a granja porcícola, Benito Juárez, *Méndez & Durán 908* (MO); rancho sobre la carr. Cancún Tulum, *Moreno C. 462* (MEXU); Isla de Cozumel, Cozumel, 5 km N de la carr. transversal, *Cabrera C. & de Cabrera 9870* (MEXU, MO); Cozumel Island, vic. of San Miguel de Cozumel, *Lewis 6868* (MO, TEX); Felipe Carrillo Puerto, Mixtequilla, 2.5 km hacia Yocdzonot Poniente, *Balam 627* (F, MO); Othón P. Blanco, 0.5 km S de Nuevo Jerusalén, *Carnevali et al. 4980* (K). **Yucatán:** betw. Thul & Becanchen, *Darwin & White 2229* (F, MEXU, MO); Yaxcobá de Tixcacaltuyub, 13 km rumbo a Peto, *Simá 358* (MEXU).

6. Gouania ferruginea A. Pool, sp. nov. TYPE: Guatemala. Sacatepéquez: Antigua, San Mateo Milpas Altas, 1900 m, 14 Aug. 1992, *M. Véliz Pérez 92.2280* (holotype, MO!; isotypes, MEXU!, BIGU not seen). Figure 10A–E.

Diagnosis. New species similar to *Gouania eurycarpa* Standl., but with lateral leaf veins 7 or 8 per side of midrib, flowers and fruits drying dark ferruginous, and fruit body width 2/5 the width of the mericarp.

Liana; young branches solid, densely villous or velutinous, trichomes ferruginous. Leaf blades 5.5–10 × 4–7 cm, ovate or elliptic, membranaceous, adaxial surface drying dark red-brown or dark green, densely to scattered villous to sericeous with trichomes 0.25–0.6 mm, light brown, abaxial surface drying pale green or pale yellow, densely villous and tomentose with trichomes 0.5–1 mm, spreading and matted, all white, or red-brown on lateral veins, lateral veins 7 or 8 per side of midrib, diverging at ca. 45° angles, base cordate then shortly decurrent or truncate, margin serrate (rarely crenate), 1 to 3 teeth/cm, tooth glands pustular to cupular at maturity, apex acute or short-acuminate; stipules 2-lobed, at least some retained into young fruit, upper lobe 2–4.5 × 1–1.5 mm, erect, lanceolate, acuminate, lower lobe 2–3.5 × 0.5–1.25 mm, curving downward, lanceolate, acuminate; petioles 5–10 mm. Inflorescence with longest racemiform part 8.5–11 cm, indumentum of rachis similar to that of young branches, bract of cyme 2.5–3 mm, lanceolate, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.75 mm, hypanthium densely villous

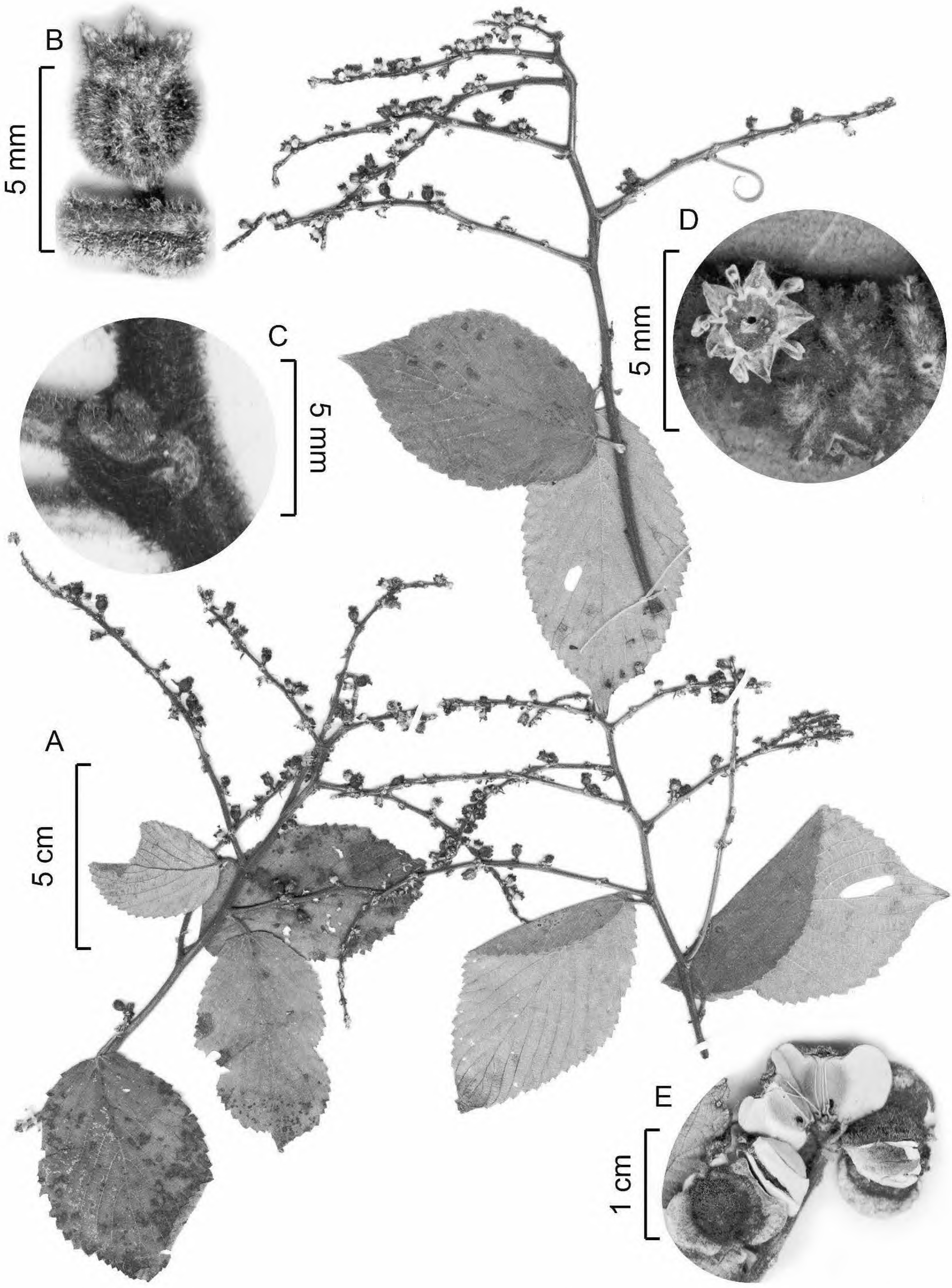


Figure 10. *Gouania ferruginea* A. Pool. —A. Three fertile branches with flowers and young developing fruits. —B. Young developing fruit. —C. Stem node with stipule. —D. Flower at inflorescence node. —E. Portion of infructescence with fruits. A–C scanned from the holotype *M. Véliz Pérez 92.2280* (MO); D scanned from the paratype *W. E. Harmon & J. D. Dwyer 2912* (MO); and E scanned from the paratype *P. C. Standley 59894* (F).

with trichomes ferruginous and white; sepals 0.9–1.25 mm, externally densely villous, trichomes ferruginous; petals 0.8–1.5 mm; stamens with filaments 0.35–0.7 mm, anthers 0.25–0.3 mm; disc excluding lobes 1.2–1.75 mm diam., glabrous, disc lobes ca. 0.25 × 0.5–1 mm at apex, transversely rectangular, generally apically bilobed, (1/5–)1/4 length of sepals; style pubescent at base. Young fruits densely velutinous, trichomes ferruginous or ferruginous and white; mature mericarps butterfly-shaped, the wings attached to apex and base of fruit body as well as sides, externally drying green but surface nearly totally obscured by indumentum, densely villous with trichomes ca. 0.25 mm, ferruginous, internally drying with wings yellow-white, contrasting only slightly with light brown fruit body, fruit body ca. 6.2 mm high, wings ca. 7.2 mm high, distance between highest points of 2 wings ca. 7 mm, width of mericarp ca. 12 mm, 2× height of fruit body, width of fruit body ca. 5 mm, 2/5 width of mericarp; seeds unknown.

Habitat and distribution. *Gouania ferruginea* is known from Guatemala (Baja Verapaz and Sacatepéquez) and Honduras (Ocotepeque). It is found in oak, pine-oak, or *Liquidambar* forest, at 1500–2200 m elevation (Fig. 5B).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania ferruginea* is known from only 10 collections from upper elevations in the mountains of Guatemala and Honduras. It has an estimated extent of occupancy of about 14,000 km² and an estimated area of occupancy of 40 km². Population studies should be conducted to determine its conservation status.

Phenology. *Gouania ferruginea* has been collected in flower in July and August.

Discussion. *Gouania ferruginea* is most similar to *G. eurycarpa*, but *G. eurycarpa* is restricted to low elevations (0–520 m) of the Yucatan Peninsula and Atlantic Honduras. The two species can be separated following the key to species; *G. eurycarpa* has fewer lateral veins on either side of midrib (usually four or five, rarely six), flowers and fruits dry externally white or yellow to brown or light red-brown, and the width of the fruit body is one fourth to one third the width of the mericarp. Specimens of *G. ferruginea* have frequently been misidentified as *G. polygama*, which differs most markedly in its mericarps, nearly glabrous and dumbbell-shaped type (vs. densely villous and butterfly-shaped in *G. ferruginea*), and flowers with the disc lobes (1/3–)2/5–3/5(–2/3) the length of the sepals (vs. the disc lobes (1/5–)1/4 the length of the sepals) and the annulus with trichomes (vs. the entire disc glabrous). In flower, *G. ferruginea* can be similar to *G. conzattii* of central Mexico. However, *G. conzattii* often has the annulus with trichomes and the young developing fruit sparsely pilose to glabrescent.

Paratypes. GUATEMALA. **Baja Verapaz:** Santa Rosa, *P. C. Standley 91084* (F). **Sacatepéquez:** Volcán de Acatenango, *M. Véliz Pérez 94.4037* (MEXU), *14159* (MO); Antigua Guatemala, en la aldea San Mateo, *J. J. Castillo Mont & M. Véliz Pérez 2775* (NY); near Pastores, *P. C. Standley 59894* (F); 5 km S of Santa María de Jesús, *W. E. Harmon & J. D. Dwyer 2912* (GH, MO); Santiago Sacatepéquez, *R. Gómez 796* (GH). **San Marcos:** Quesiguán, *J. R. Johnston 1258* (F). HONDURAS. **Ocotepeque:** Sinuapa, 17 km NE of Nueva Ocotepeque, *W. E. Harmon & J. D. Dwyer 3788* (MO).

7. Gouania guiengolensis A. Pool, sp. nov. TYPE: Mexico. Oaxaca: Tehuantepec, ruinas del Cerro Guiengola, 450 m, 3 Sep. 1985, *M. L. Torres C., R. Torres C. & C. Martínez R. 134* (holotype, MEXU!; isotype, MO!). Figures 1B, 2F, 11A–D.

Diagnosis. New species similar to *Gouania rosei* Wiggins but with linear stipules, glabrous mericarps, and fruit body width 3/5 width of mericarp.

Liana; young branches solid, densely to sparsely pilose to sericeous, trichomes white to light red-brown. Leaf blades 4.5–10.2 × 2.5–5 cm, lanceolate to ovate, membranaceous, adaxial surface drying dark green to light green, sparsely pubescent, or glabrescent and trichomes retained only on venation with trichomes 0.25–0.5 mm, appressed, white, abaxial surface drying pale green, abundantly villous to pilose to glabrescent and trichomes retained only on venation with trichomes 0.2–0.5 mm, white, lateral veins 4 to 6 per side of midrib, diverging at 50°–70° angles, base cordate then shortly decurrent or truncate, margin serrate to serrulate or crenate to crenulate, 1 to 3 teeth/cm, tooth glands cupular, apex acute or acuminate; stipules unlobed (Fig. 1B), usually lost at anthesis, 5–9 × 0.5–0.75 mm, flexuous, linear; petioles 7–20 mm. Inflorescence with longest racemiform part 4–9 cm, rachis villous to sericeous with trichomes light red-brown, bract of cyme 1.75–5.5 mm, linear, cymes appearing sessile, mature flowers appearing sessile to pedicels to 1 mm, hypanthium densely villous to sericeous with trichomes yellow-white to white; sepals 0.7–1.1 mm, externally densely to sparsely villous to sericeous, trichomes yellow-white to white; petals 0.75–1.1 mm; stamens with filaments 0.5–0.8 mm, anthers 0.2–0.25 mm; disc excluding lobes 1–1.25 mm diam.,

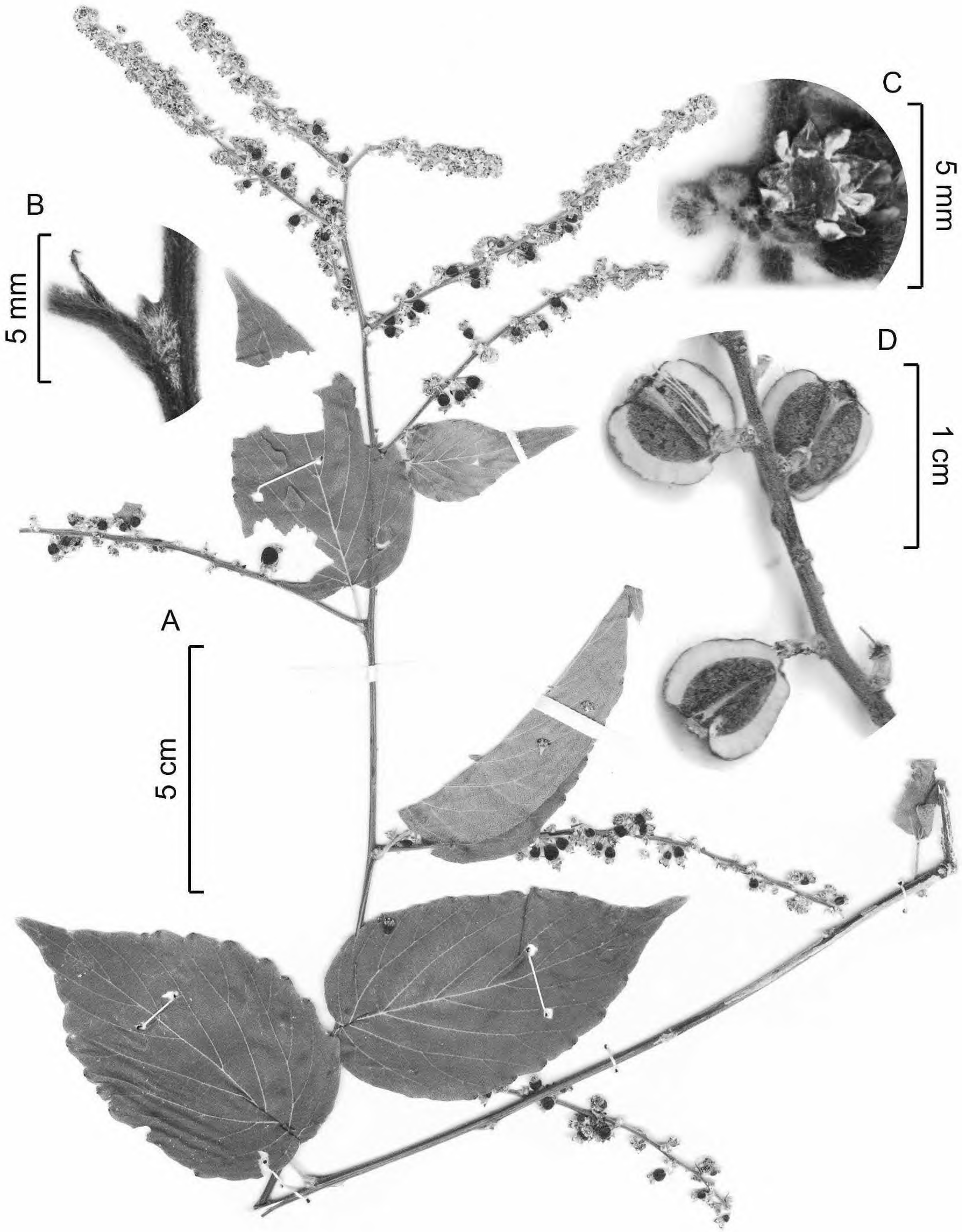


Figure 11. *Gouania guiengolensis* A. Pool. —A. Fertile branch with flowers and young developing fruits. —B. Stem node with stipule. —C. Flower at inflorescence node. —D. Portion of infructescence with open fruits. A scanned from the holotype *M. L. Torres C., R. Torres C. & C. Martínez R. 134* (MEXU); B, C scanned from the isotype *M. L. Torres C., R. Torres & C. Martínez R. 134* (MO); and D scanned from the paratype *M. L. Torres C. et al. 580* (MEXU).

annulus with numerous to few trichomes, disc otherwise glabrous, disc lobes ca. 0.2–0.4 × 0.35–0.5 mm at apex and transversely rectangular (rarely lanceolate and acuminate, *E. Matuda 586*), generally apically bilobed, 1/4–1/3(–1/2) length of sepals; style glabrous or pubescent at base. Young fruits sparsely pilose, trichomes white; mature mericarps butterfly-shaped (Fig. 2F), the wings attached to apex and base

of fruit body as well as sides, externally drying dark red-brown, glabrous or with few minute trichomes retained at apex of fruit body, internally drying yellow-white on wings strongly contrasting with dark red-brown fruit body, fruit body 5–6 mm high, wings 6–7.5 mm high, distance between highest points of 2 wings ca. 4 mm, width of mericarp 7–8 mm, 1–1.5× height of fruit body, width of fruit body 4–5 mm, 3/5 width of mericarp; seeds 3.5–4 × 2.5–3.5 mm, shiny brown.

Habitat and distribution. *Gouania guiengolensis* is known from the Pacific area of the Isthmus of Tehuantepec, Mexico (Oaxaca), with a number of collections from Cerro Guiengola. It is found in deciduous forests, often in secondary vegetation, at 30–720 m elevation (Fig. 4B).

Phenology. *Gouania guiengolensis* has been collected in flower from July to September.

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania guiengolensis* is known from 18 collections made from four different districts in the Pacific area of the Isthmus of Tehuantepec on and near Cerro Guiengola. Its estimated extent of occupany is ca. 7175 km^2 and the estimated area of occupancy is 56 km^2. As 93% of the collections fall outside of protected areas, it can be assumed that this species is either endangered or vulnerable; therefore further study is urgently called for.

Discussion. *Gouania guiengolensis* is most similar to the more widespread *G. rosei* (Pacific Mexico from Baja California and Sonora to the Tehuantepec District of Oaxaca). Both species have unlobed stipules, the abaxial surface of the leaves villous to pilose, flowers which at least sometimes (variable in *G. rosei*) have trichomes along the disc annulus and mericarps with the internal surface drying bicolored. They differ in the shape of the stipules, mericarp pubescence, and the ratio of the width of the fruit body to that of the mericarps. In *G. guiengolensis*, the stipules are linear, the mericarps glabrous, and the width of fruit body three fifths the width of mericarps; in *G. rosei*, the stipules are lanceolate, the mericarps densely pubescent, and the width of fruit body to one half that of the mericarps. The mericarps of *G. guiengolensis* are also a little higher, with the fruit body 5–6 mm (vs. 4–5 mm in *G. rosei*) and wings 6–7.5 mm (vs. 4–6 mm).

Most specimens of *Gouania guiengolensis* were previously identified as *G. lupuloides*, which differs in having bilobed stipules, with the upper lobe acuminate and lanceolate or triangular. In *G. lupuloides*, the flowers have the disc completely glabrous, the mericarps (8)9–16 mm wide and 1.5–3.2× the height of the fruit body, and the width of the fruit body (1/5)1/4–1/2 that of the mericarps, and mericarps drying nearly unicolored on the internal surface. One collection of *G. guiengolensis* (*Matuda 586*) is unusual in having the disc lobes lanceolate and acuminate and could be confused with *G. polygama*. It can be recognized as *G. guiengolensis* by its linear, unlobed stipules (Fig. 1B) and linear cyme bracts.

Paratypes. MEXICO. **Oaxaca:** 1 km al N de Ojo de Agua, *E. F. Cabrera C. & H. de Cabrera 7387* (MEXU); Distr. Juchitán, Mpio. Asunción Ixtaltepec, Cerro Timbón, *A. Saynes V. & A. Sánchez M. 3461* (MEXU), a 1 km en línea recta al NE (32°) de Nizanda, *C. Gallardo H. et al. 1525* (MEXU), cercanas a la vía del tren Transístmico, *E. A. Pérez G. & B. Reyes D. 1604* (MEXU, MO), Cerro Verde, *E. A. Pérez G. 1799* (MO); Distr. Juchitán, Ruta 185, la Ventosa a Matías Romero, *D. H. Lorence & R. Cedillo T. 3040* (F); Distr. Pochutla, Mpio. San Miguel del Puerto, Majahual, *M. Elorsa C. 642* (MEXU, TEX), Zimatán, 3 km LR N del puente, por el Chorro, *S. H. Salas M. & E. M. Martínez S. 2136* (MEXU), Zimatán, 4.5 km N del puente, por la brecha a Xadani, *S. H. Salas M. et al. 1843* (MEXU, MO); Distr. Tehuantepec, Tehuantepec, *E. Matuda 586* (MEXU, MICH, MO; Fig. 1B), Rincón Bamba a Garrapatero, Rincón Bamba, *C. Martínez R. 1813* (F, MEXU, MO, NY, TEX), Mpio. Salina Cruz, Cerro Marimba, entrando por Rincón Bamba, *C. Martínez R. 1024* (F, MEXU, MO, NY, TEX), 10 km al W de la Chiviza, camino a Lachiguiri, *R. Torres C. & C. Martínez R. 5739* (MEXU); Distr. Tehuantepec, Ruinas del Cerro Guiengola, *M. L. Torres C. et al. 580* (MEXU, MO; Fig. 2F), ladera S, *M. L. Torres C. et al. 689* (MEXU, MO), ladera O, entrando por el Mármol, "Arroyo de Piedra," *M. L. Torres C. et al. 238* (MEXU, MO), ladera S, *M. L. Torres C. et al. 180* (MEXU, MO).

8. Gouania hypoglauca Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 89. 1940. TYPE: Costa Rica. Alajuela, Cantón de San Carlos, Villa Quesada, edge of Caribbean rain forest, 14 Apr. 1939, *A. Smith F1952* (holotype, F!; isotypes, MO!, NY!, US!). Figure 2G.

Liana; young branches hollow or solid, densely tomentose, trichomes ferruginous. Leaf blades 3.7–12 × 2.5–5.6 cm, ovate or elliptic, membranaceous to subcoriaceous, adaxial surface drying dark brown or black, abundantly to sparsely pubescent or trichomes often restricted to venation, glabrous with age, with trichomes 0.2–0.75 mm, ± straight and appressed, white, abaxial surface drying gray, yellow-gray or grayish yellow-green, surface between venation totally covered with trichomes 0.05–0.1 mm (sometimes glabrescent with trichomes retained only at base in older leaves), and on venation to 0.25 mm, all trichomes straight and appressed, all white, or red-

brown on venation, lateral veins (2)3 or 4(5) per side of midrib, diverging at 60°–75° angles, base rounded or rounded then shortly decurrent to obtuse (rarely cordate to subcordate), margin crenulate to nearly entire, 1 tooth/cm, tooth glands shallowly to deeply cupular (rarely pulvinate), apex short-acuminate; stipules unlobed or with small foot, caducous, 1–3.5 × 0.5–1.5 mm, erect, usually tightly appressed to branch (less frequently upward spreading), triangular to narrowly triangular, acuminate, foot (if present) 0.25–1 × 0.2–0.5 mm, curving downward, subulate; petioles 5–15 mm. Inflorescence with longest racemiform part 9–21 cm, rachis tomentose with trichomes white or ferruginous or pilose with trichomes ferruginous, bract of cyme 1–2 mm, subulate to triangular, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.25(0.75) mm, hypanthium and sepals externally tomentose or sericeous with trichomes white or green-white, sometimes mixed with ferruginous; sepals 0.6–1.1 mm; petals 0.7–1.25 mm; stamens with filaments 0.5–0.75 mm, anthers 0.2–0.25 mm; disc excluding lobes 1–1.9 mm diam., with numerous trichomes along annulus and most of disc excluding, or often including, lobes rarely pubescent only along annulus (*Webster & Dressler 16722*) or along annulus and extending by rays onto disc (*de Nevers 5803*), disc lobes 0.1–0.3(0.5) mm × 0.3–0.75 mm at apex, transversely rectangular, generally apically bilobed, 1/6–1/3 length of sepals (rarely oblong and 1/2 length of sepals, *de Nevers 5803*, *Mori & Bolten 7106*); style pubescent. Young fruits densely to abundantly velutinous to tomentose and villous, trichomes ferruginous or white; mature mericarps butterfly-shaped (Fig. 2G), the wings attached to apex and base of fruit body as well as sides, externally drying dark brown or lighter on wings, abundantly tomentose with trichomes 0.05–0.25 mm, white to ferruginous, internally drying yellow-white on wings, not, or only slightly, contrasting with very light brown fruit body, fruit body 6–12 mm high, wings 9–14 mm high, distance between highest points of 2 wings 4–7(10) mm, width of mericarp 10–15.3(17) mm, 1.5–2× height of fruit body, width of fruit body 3.5–5 mm, 1/4–1/2 width of mericarp; seeds 3.25–4.5 × 2.25–3.5 mm, shiny brown.

Iconography. Krings and Braham (2005: 126, tab. 10.1, fig. B).

Habitat and distribution. *Gouania hypoglauca* is known from southeast Nicaragua, Costa Rica, and Panama. It is found in wet to very wet evergreen forests, between 0 and 1000 (rarely to 1400) m elevation (Fig. 6B).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania hypoglauca* is known from 58 collections made in wet to very wet forests of southeastern Nicaragua to central Panama. It has an estimated area of occupancy of ca. 192 km^2. Further studies need to be conducted to estimate its conservation risks.

Phenology. *Gouania hypoglauca* has been collected in flower from May to September.

Discussion. The dense covering of the abaxial leaf surfaces with minute, appressed trichomes distinguishes *Gouania hypoglauca* from all other Central American species. It is most similar to *G. discolor* Benth. (of Amazonian South America: Brazil, Colombia, Guyana, and Venezuela) that differs in the flowers having longer pedicels, (1.5)2.5–3 mm, the disc trichomes usually restricted to the annulus (rarely extending by rays onto disc), the disc lobes one half to three fourths the length of the sepals, and usually lanceolate, acuminate, and the inner surface of the mericarps with numerous, dark red-brown rays extending from the fruit body onto the wings. Several specimens of *G. hypoglauca* from Panama approach *G. discolor*, namely *Webster & Dressler 16722* (with trichomes of disc restricted to annulus), *de Nevers 5803* (trichomes along annulus extending by rays onto disc and disc lobes 1/2 the length of the sepals) and *Mori & Bolten 7106* (disc lobes 1/2 the length of the sepals).

Additional specimens examined. COSTA RICA. **Alajuela:** Zapote de Alfaro Ruz [Ruiz], finka [finca] los Ensagos [Ensayos], *Barquero M. s.n.* [Aug. 1969] (NY, US); San Ramón, 2–3 km NW of Bajo Rodríguez, *Utley & Utley 5138* (F, MICH, MO); Upala, P. N. Guanacaste, Cordillera de Guanacaste, Est. San Ramón, Dos Ríos, *Espinoza 801* (CAS, MO); Upala, C. B. Guanacaste-Rincón de la Vieja, Cuenca del Pizote, San Cristóbal, *Quesada 476* (MO); Zarcero, ca. 8 mi. S of Quesada, *Webster et al. 12211* (TEX). **Guanacaste:** P. N. Rincón de la Vieja, Sendero a San Jorge, *Rivera 1366* (MO); Volcán Miravalles, trail SE lower slopes near Río Naranjo, *Wilbur & Almeda 16620* (F), *16664* (CAS, F, LL, MICH, MO); La Cruz, P. N. Guanacaste, Volcán Orosí, Est. Pitilla, *Moraga 924* (MO); Liberia, Rincón de la Vieja, *Barringer et al. 4059* (F, MO, TEX); Tilarán, P. N. Volcán Tenorio, Cuenca del San Carlos, Sect. Nevera, *Chaves 539* (G, MO, NY). **Heredia:** 3 mi. S of Cariblanco, *Croat 35776a* (MO); P. N. Braulio Carrillo, Est. Magsasay, Sarapiquí, *Acevedo 92* (MO); Sarapiquí, Cuenca del Sarapiquí, Finca Aracuak, Río Frío, *Kriebel 736* (MO); La Selva Biol. Stat., *Chacón G. 964* (F, MO), *Jacobs 2068* (MO), *Smith 251* (CAS, F, MICH, MO), *Sperry 742* (F, LL), *Vargas 1790* (MO), Río Puerto Viejo just E of jct. w/ Río Sarapiquí, *Smith 1091* (CAS, F, MO). **Limón:** Parque Tortuguero, Est. Agua Fría, *Robles 1127* (BM, F, MO, NY, TEX); vic. U.S. Dept. Agric. Rubber Exp. Stat., Los Diamantes, *Holm & Iltis 338* (BM, F, NY); Livingston on Reventazon, Bonilla, Llanura de Santa Clara along Río

Reventazón, *Rowlee & Stork 688* (NY), *719* (NY, US); Pococí, R. N. F. S. Barra del Colorado, Llanura de Tortuguero, Sardinas, *Araya 52* (MO); Pococí, R. N. F. S., Barra del Colorado, Llanura de Tortuguero, Puerto Lindo, *Araya & Corrales 795* (MEXU, MO); Talamanca, R. N. V. S., Gandoca-Manzanillo, faja costeña de Limón, Manzanillo, *Rodríguez G. 542* (MO); Talamanca, Bri brí, 7 km NO del pueblo, *Cascante 546* (F, K). **Puntarenas:** Golfito, P. N. Corcovado, Valle de Coto Colorado, Est. Esquinas, secc. Esquinas, *Aguilar 3276* (MO); Golfito, entre Golfito y Villa Briceño, *Hammel 18513* (MO); Golfito, Res. For. Gulfo Dulce, entre Rancho Quemado y Drake, *Aguilar et al. 116* (MO); Res. For. Golfo Dulce, Aguabuena sect. cuenca norte, *Aguilar 585* (MO); Osa, R. F. Golfo Dulce, de Rancho Quemado a Drake, *Hammel 21057* (G); Osa, R. F. Golfo Dulce, Bahía Chal, Los Mogos, *Ramírez & Morales 332* (MO); Osa, camino de Altura, 2–5 mi. W Rincón de Osa, *Raven 21503* (MO). **San José:** Tarrazú, Los Llanos de Santa María, Filas Las Rejas, *Valverde et al. 83* (K); Tarrazú, Faja Costeña del Valle de Parrita, *Vargas 464* (MO). NICARAGUA. **Atlántico Sur:** camino entre San Antonio y San Martín, *Araquistain 3140* (MO); 3 km E de La Esperanza, *Araquistain 3169* (MO, TEX); Monkey Point, Caño El Pato, *Moreno 12469-a* (MO), *Moreno 12408* (MO; Fig. 2G); a lo largo del Río Punta Gorda, entre el poblado de Nueva Atlanta y la desembocadura del mismo, *Rueda et al. 3083* (MO). **Río San Juan:** Buena Vista, 1 km W de Delta del Río San Juan, *Martínez S. & Riviere 2074* (F); Mpio. El Castillo, commun. Filas Verdes, de la casa de Juan Mayorga, *Jirón 25* (MO); Sábalo, 1 km al N de Río San Juan, *Moreno 26087* (MO); en el trecho entre San Juan del Norte y La Casa de Ramón Castillo, sobre el Caño San Juanillo, *Rueda et al. 1758* (MO); sobre el Río Indio, entre San Juan del Norte Nuevo y La Casa de Narciso Orozco, *Rueda et al. 1585* (MO); Res. Indio-Maíz, Mpio. San Juan del Norte, *Rueda et al. 4654* (MO). PANAMA. Western Panama, *Stork 34* (US). **Bocas del Toro:** 4–6 mi. N of Almirante, *McDaniel 5103* (MO); Changuinola, *Dunlap 235* (F, NY, US). **Coclé:** El Valle, behind Pensión, *Ebinger 961* (MO). **Colón:** Santa Rita Ridge, 2–3 mi. from Transisthmian Hwy., *Gentry 1864* (MO, US); al E de la zona montañosa de Santa Rita, *Correa A. & Dressler 986* (MO, NY, US); Santa Rita Ridge, rd. to Est. Calibrar Lluvia el Agua Clara, *Webster & Dressler 16722* (LL). **Panamá:** vic. Cerro Jefe, *McPherson 9993* (MO); Chepo, El Llano–Cartí rd., 9–12 km from Panamerican Hwy., *D'Arcy 10634* (MO); Cerro Azul area, 22 km from Pan American Hwy., *Mori & Bolten 7106* (MO). **San Blas:** El Llano–Cartí rd., betw. Río Pingandí & Río Cartí Grande, *de Nevers 5803* (MO, NY, TEX, US).

9. Gouania lupuloides (L.) Urb., Symb. Antill. 4: 378. 1910. Basionym: *Banisteria lupuloides* L., Sp. Pl. 1: 427. 1753. *Gouania domingensis* L., Sp. Pl. (ed. 2), 2: 1663. 1763. *Lupulus lupuloides* (L.) Kuntze, Revis. Gen. Pl. 1: 119. 1891, as "*lupulodes*." *Lupulus lupuloides* var. *domingensis* (L.) Kuntze, Revis. Gen. 1: 119. 1891. TYPE: tab. 201, fig. 4 in Plukenet, Phytographia, 3. 1692 (lectotype, designated here, Plukenet, tab. 201, fig. 4. in Plukenet, 1692!). EPITYPE: Barbados. Kendal Gully, 24 Mar. 1937, *A. E. S. McIntosh 333* (epitype, designated here, K!). Figures 1C–G, 2H.

Rhamnus domingensis Jacq., Enum. Syst. Pl. 17. 1760. *Gouania glabra* Jacq., Select. Stirp. Amer. Hist. 264. 1763. TYPE: tab. 179, fig. 40 in Jacq., Select. Stirp. Amer. Hist. 1763 (neotype [for *Rhamnus domingensis*] and lectotype [for *Gouania glabra*], both equivalent names) designated here, Jacquin, tab. 179, fig. 40 in Jacquin, 1763!).

Gouania cyclocarpa Sm. in Rees, Cycl. 16 (II). *Gouania* No. 3. 1819 [1811], syn. nov. TYPE: West Indies? s. loc., s.d., s. coll., "*Gouania cyclocarpa n. 3, Sm. in Rees Cycl.*" (holotype, Smith Herbarium LINN not seen, microfiche 1595 no. 3!).

Gouania pubescens Poir. var. *martinicensis* Poir., Encycl., Suppl. 2, 820. 1811 [1812], as "[var.]? Gouania (martinicensis)," syn. nov. TYPE: tab. 845, fig. 1, h and i in Lam., Tabl. Encycl. 1793 [1799] (lectotype, designated here, Lamarck, tab. 845, fig. 1, h and i in Lamarck, 1793 [1799]!).

Gouania glabriuscula Stokes, Bot. Mat. Med. 1: 436. 1812. TYPE: Jamaica, s. loc., s.d., *W. Wright s.n.* (lecotype, designated here, NY!; isolectotypes, GH!, K!).

Gouania lupuloides var. *aptera* Urb., Symb. Antill. 4: 378. 1910, syn. nov. TYPE: Puerto Rico. "Inter Coamo et Aibonito ad viam," 4 Nov. 1885, *P. Sintenis 1960* (lectotype, designated here, US!; isolectotypes, BM!, GH!, K!).

Gouania viridis Brandegee, Univ. Calif. Publ. Bot. 6: 501. 1919. TYPE: Mexico. Veracruz: Zacuapan, Oct. 1917, *C. A. Purpus 8032* (holotype, UC not seen, digital image!; isotypes, GH!, MO!, NY!, US!).

Gouania lupuloides var. *parvifolia* Hadač, Folia Geobot. Phytotax. 5: 431. 1970, syn. nov. TYPE: Cuba. Las Villas: Playa Larga, 0.5 km ad boreum a balneis, 22 Dec. 1967, *E. Hadač 838* (holotype, PR!).

Liana; young branches solid or hollow, densely to sparsely pilose or sericeous (rarely tomentose), trichomes white or red-brown. Leaf blades 4–13.2 × 2–8(9.2) cm, elliptic to ovate or lanceolate, membranaceous, adaxial surface drying green or less frequently brown-green (rarely red-brown), abundantly pubescent to glabrescent, sometimes trichomes only on venation, with trichomes 0.2–1 mm, usually appressed, straight and ascending, sometimes some or all spreading, slightly curved or kinky but still appressed, white or yellow-white (rarely red-brown), abaxial surface drying similar color to adaxial surface to slightly paler, densely pubescent to glabrescent, sometimes trichomes only on venation, with trichomes 0.15–1 mm, appressed, straight and ascending, or some or all somewhat curving or kinky or straight and spreading in all directions including erect, overall or only on veins or vein axils, white or yellow-white (rarely red-brown), lateral veins (3)4 or 5, or less frequently 6 per side of midrib, diverging at 45°–60°(70°) angles, base subcordate, rounded or cordate and then usually shortly decurrent, margin serrate to serrulate to nearly entire, irregularly serrate or 1 to 3(4) teeth/cm, tooth glands cupular (rarely pulvinate), apex acuminate or cuspidate (rarely acute); stipules 2-

lobed, usually retained (at least in part) into fruiting upper lobe 1–10 × 0.5–3 mm, curving upward or erect, lanceolate, acuminate and the tip long extended and flexuous (Fig. 1D–G) or triangular, acuminate, firm (Fig. 1C), lower lobe 0.1–14 mm, curving downward or spreading, lanceolate, acuminate (Fig. 1D), linear, subulate (Fig. 1C), oblong, or foliaceous and ovate (Fig. 1E), circular, broadly rectangular, or reniform, sometimes with long-extended glandular tip or with 2 or 3 short (Fig. 1F) to long-extended glandular teeth (Fig. 1G); petioles 3–26 mm. Inflorescence with longest racemiform part 7–25 cm, rachis sparsely to densely pilose or tomentose with trichomes white or yellow-white, or red-brown, bract of cyme 1.2–4(–7) mm, lanceolate, acuminate, cymes appearing sessile (rarely peduncle to 1.5 mm), mature flowers with pedicels (0.5–)1–3(–4) mm, hypanthium sparsely to densely sericeous (rarely tomentose) with trichomes white, yellow-white or light red-brown to ferruginous; sepals (0.5–)0.75–1.6 mm, externally sparsely to abundantly sericeous, trichomes white, yellow-white or light red-brown to ferruginous; petals (0.5–)0.6–1.5 mm; stamens with filaments (0.25–)0.3–1.2 mm, anthers (0.15–)0.2–0.3 mm; disc excluding lobes 1–1.8(–2.1) mm diam., glabrous, disc lobes (0.1–)0.2–0.5 × (0.1–)0.2–0.75 mm at apex, square to transversely rectangular (rarely longer than wide and narrowing apically, very rarely to point), generally apically bilobed, 1/5–2/5(1/2) length of sepals; style glabrous (rarely with trichomes). Young fruits glabrescent to sparsely pilose or sericeous, trichomes white to light red-brown; mature mericarps butterfly-shaped (Fig. 2H), the wings attached to apex and base of fruit body as well as sides, externally drying yellow-brown, green-brown, red-brown, or yellow, darker brown over fruit body, glabrous or apically sparsely and minutely pilose, puberulent, or sericeous with trichomes 0.1–0.3 mm, white, internally drying off-white on wings, slightly or moderately contrasting with slightly darker off-white to beige fruit body, fruit body 4–7 mm high, wings (5)6.6–12 mm high, distance between highest points of 2 wings 3–7 mm, width of mericarp (8)9–16 mm, 1.5–3.2× height of fruit body, width of fruit body 3–4.5(5) mm, (1/5)1/4–1/2 width of mericarp; seeds 2.7–3.8 × (1.5)2–3 mm, shiny brown.

Iconography. Krings and Braham (2005: 126, tab. 10.1, fig. C, a, b, excluding c); Acevedo-Rodríguez (2003: 364, tab. 144, fig. A–H); Liogier (1994: 83, tab. 71-3); Bornstein (1989: 163, tab. 69, fig. b, excluding a); Liogier (1982: 62, tab. 13, fig. A, B, excluding C).

Habitat and distribution. *Gouania lupuloides* is known from the southeastern United States (Florida), from northern Mexico to northern Panama, and in the Caribbean basin from the Bahamas, Greater Antilles, Leeward Islands, Windward Islands, and Barbados. It is most commonly found in dry vegetation, collected from roadside thickets, cinder slopes with low shrubs, pasture on mesa with basalt outcrops, dry forest, oak forest, scrub forest on limestone, sub-deciduous or deciduous forest, open oak woodland, as well as pine and oak forest, but is also on occasion noted in moist, sub-evergreen or evergreen forests, from 0 to 1700 (rarely to 2300) m elevation (Figs. 3, 7A, 8A).

IUCN Red List category. Assessed as Least Concern (LC) by IUCN (2012) criteria, *Gouania lupuloides* is very common in a variety of habitats from coastal Florida and northern Mexico to northern Panama and throughout the islands of the Caribbean region.

Phenology. *Gouania lupuloides* has been collected in flower from August to February (rarely March to May or July).

Discussion. Linnaeus published *Banisteria lupuloides* (the basionym of *Gouania lupuloides*) in 1753, making it the name with the earliest priority in the genus *Gouania*. As such, the name *G. lupuloides* has been frequently misapplied to a wide variety of distinct species. *Gouania lupuloides* and its synonyms are typified here to aid in the correct applications of these names.

Linnaeus (1753: 427) cited for *Banisteria lupuloides* the following: "Paullinia foliis simplicibus lanceolatis serratis *Hort. Ups. 9*; Lupulus sylvestris Americana claviculis donata. *Pluk. alm. 229. t. 201. f. 4. & t. 163. f. 3. Habitat in Barbados*." Linnaeus in Hortus Upsaliensis (1748: 97) also cited the Plukenet plates, the second as "*162, f. 3*." Material available for lectotype selection consisted of the specimen at the Linnaean herbarium (1226.1, LINN) labeled in Smith's hand "*Gouania domingensis/glabra*" and in Linnaeus' hand "HU 1," the two Plukenet figures, and the specimens in Herb. Sloane 95: 197 and 99: 205 (both associated with Plukenet tab. 162, fig. 3) and 96: 158 (associated with Plukenet tab. 201, fig. 4). All the specimens are sterile, as is Plukenet tab. 162, fig. 3, while Plukenet tab. 201, fig. 4 includes a mericarp, and is therefore chosen as the lectotype. The mericarp illustrated is butterfly-shaped and the leaves illustrated have five lateral veins on either side of the midrib, both characteristics associated with *G. lupuloides*. To further clarify the application of this name, a specimen collected in Barbados, *A. E. S.*

McIntosh 333 (K), was selected as an epitype. This specimen has characteristics typical for the species: butterfly-shaped mericarps, leaves with five lateral veins per side of the midrib, and retained stipules. *Gouania lupuloides* is the only species of *Gouania* known from Barbados (Table 4).

The publication of *Gouania domingensis* L. (Linnaeus, 1763) included all the original elements cited for *Banisteria lupuloides* (note, the second Plukenet tableau mistakenly cited as 63 vs. 163 in 1753 and 162 in 1748), but this name is probably not technically superfluous as *B. lupuloides*, in 1763, had no holotype, syntypes, designated lectotype, or conserved type, and the name itself (*B. lupuloides*) was not specifically cited by Linnaeus (1763) (see Art. 52.2, ex. 12, McNeill et al., 2012). However, the name *B. lupuloides* is indirectly referred to by Linnaeus (1763) including in his phrase name "*Banisteria*" and citing the place of publication with the page number of *B. lupuloides*. The lectotype (Plukenet tab. 201, fig. 4) and epitype (*A. E. S. McIntosh 333*, K) chosen above for *B. lupuloides* are here also selected for *G. domingensis* L.

Jacquin (1760) published two species of *Rhamnus* without indication of types and with identical short descriptions, except that *R. polygama* was described as having tomentose leaves and *R. domingensis* as having glabrous leaves. Subsequently, Jacquin (1763) published the new genus *Gouania* with two species (*G. tomentosa* and *G. glabra*), noting their previous treatment in the genus *Rhamnus*, the one described with glabrous leaves, *G. glabra*, equivalent to (but not superfluous for) *R. domingensis*, as this name was not explicitly cited in Jacquin, 1763 (see Art. 52.2, McNeill et al., 2012). The locality of *G. glabra* is cited as "sylvaticis Domingensibus" (Jacquin, 1763: 264) and a plate provided, consisting of one leaf with five lateral veins on each side of the midrib, one fruit, a mericarp of the butterfly-shape, and a seed. As no Jacquin specimens of *R. domingensis/G. glabra* were found in this study (or by Urban, 1921), and as Bornstein (1989) suggests that a type specimen is not extant, the plate is chosen as the neotype of *R. domingensis* and lectotype of *G. glabra*. The illustration of the mericarp and number of blade lateral veins supports placement of these names in synonymy of *G. lupuloides*, following Urban (1910).

Smith (1819 [1811]) published *Gouania cyclocarpa* based on a specimen in his herbarium. The place of collection is cited by Smith (1819 [1811]) as from the West Indies with uncertainty. The fruits of the specimen are young, but the mericarps seem to be of the butterfly shape and the mature leaves are described as glabrous. Assuming this is from the West Indies, it is *G. lupuloides*.

Poiret (1811 [1812]: 820) published *Gouania pubescens* with a type variety (from "Saint-Domingue") and a second variety, *G. pubescens* var. *martinicensis* (from Martinique). See discussion below *G. polygama* for the placement of *G. pubescens* var. *pubescens*. Poiret (1811 [1812]) separated *G. pubescens* var. *martinicensis* from the typical variety based on its subglabrous leaves, and cited a specimen from Martinique at Herb. Desfont. For the species, he cited a plate in Lamarck, 1793 [1799] (tab. 845, fig. 1). There is no specimen labeled with the name *G. pubescens* var. *martinicensis* in the microfiche collection at P-LA, nor was a specimen found when requested from FI. The plate cited represents two different species, with the flowering specimen (1799: tab. 845, fig. 1 a–g) being *G. polygama*, while the close-ups of the fruit depicted before (1799: tab. 845, fig. 1 i) and after the mericarps have separated (1799: tab. 845, fig. 1 h) correspond to *G. lupuloides*. As *G. lupuloides* is the only species of *Gouania* known from Martinique (Table 4), and as figures i and h are of *G. lupuloides* and no specimens of *G. pubescens* var. *martinicensis* can be found, these figures are chosen as the lectotype of *G. pubescens* var. *martinicensis*, which is also placed in synonymy under *G. lupuloides*. This variety was treated by Suessenguth (1953a: 170, as *G.* "*martinicensis*") as a synonym of *G. polygama*.

Stokes published *Gouania glabriuscula* in 1812 based on a Dr. Wright collection from Jamaica in young fruit. I have seen no collections labeled *G. glabriuscula*, and have not been able to find the Stokes herbarium, which, in 1856, was auctioned by Sotheby and is now untraceable as such (Kent & Allen, 1984). However, I have seen a number of specimens with young fruit labeled "Jamaica, Dr. Wright, Herb. Forsyth., Purchased 1835," and these are assumed to be isotypes. They are all *G. lupuloides*, which is the only species of *Gouania* known from Jamaica. The Dr. Wright is William Wright, not Charles Wright, who did not collect in Jamaica. All are mounted on the same sheet as other specimens that cannot be the type. On the GH sheet, the type of *G. glabriuscula* is only the thyrse mounted on the far left side of the sheet. On the same sheet are two specimens of *G. polygama*, both in young fruit, collected by C. Wright in Cuba. On the K sheet, the type material is in the center; to the left is a flowering collection by W. Wright from Jamaica, and on the right a specimen from St. Lucia collected by A. Anderson; all three are *G. lupuloides*. On the NY sheet, the type is on the left; the specimen on the

right (also *G. lupuloides*) was collected on St. Vincent, the collector's name being illegible. In lieu of finding the Stokes collection, the NY sheet is selected as the lectotype, as it has the most complete leaf.

Urban (1910) published *Gouania lupuloides* var. *aptera* based on two young fruiting collections (*P. Sintenis 1960* and *A. Stahl 782*) and a further one in bud and flower, *P. Sintenis 2211*. I have seen images of the isosyntype, *A. Stahl 782* (HBG), and syntype, *P. Sintenis 2211* (L), and studied the specimens of syntypes *P. Sintenis 1960* (BM, GH, K, US). *P. Sintenis 1960* has the most duplicates available for study, and of these duplicates the diagnostic characters of number of lateral leaf veins and shape of stipule lobes are most easily observed on the US sheet, which is therefore selected as the lectotype. The number of leaf lateral veins, retained stipules, and size of the larger immature fruits support placement of this name in synonymy of *G. lupuloides*.

Considerable consideration was given to evaluating *Gouania viridis*, published in 1919 by Brandegee. Four of the isotypes (*C. A. Purpus 8032*, GH, MO, NY, US) were studied and they, and a number of specimens from primarily low elevation (0–500[900] m) in Caribbean Mexico (Veracruz [e.g., *Ventura A. 2695*], eastern Oaxaca [e.g., *Martínez Calderón 1601*], and Tabasco [e.g., *Calónico S. et al. 21428*]), but extending north to San Luis Potosí (e.g., *Deam 49*), west to Guerrero (e.g., *Kruse 1425*) and central Chiapas (e.g., *Soto N. et al. 13493*), and south to Cortés Department of Honduras (e.g., *Williams & Williams 18809*), share a number of characteristics otherwise unusual in *G. lupuloides*: abaxial surface of leaves either pilose or with straight trichomes extending at right angles to surface, stipules with the upper lobe narrowly triangular, firm and erect and not at all flexuous and the lower lobe extending straight downward and subulate to linear and frequently lost (Fig. 1C), and short stamen filaments, 0.3–0.5 mm long and equal in length to twice as long as anthers. These stipule and stamen characteristics are individually found scattered throughout the range of the species in southern Mexico, Central America, and the West Indies, while concentrations of specimens with pilose or straight trichomes extending at right angles to the leaf surface are found mainly in middle to upper elevations of central Guatemala (850–1900 m) and in Hispaniola. Within the group sharing the viridis characteristics, those specimens from the more eastern part of the range (e.g., *Purpus 2274*, Veracruz, Mexico) have ferruginous trichomes on the sepals, while those from further west (e.g., *Reyes-García & Urquijo 890*, Chiapas, Mexico) have the more typical yellow-white trichomes. While the variation in these characters is noteworthy, it is not consistent enough to warrant taxonomic recognition. The placement of *G. viridis* in synonymy of *G. lupuloides* follows Fernández (1986).

Hadač (1970) published *Gouania lupuloides* var. *parvifolia*. I have studied the holotype and it fits well within the species concept of typical *G. lupuloides* employed here, thus the name is placed in synonymy.

Usually the disc lobes of *Gouania lupuloides* are 1/5 to 2/5 the length of the sepals and are apically as wide to twice as wide as long and do not taper. However, occasional specimens (e.g., *Durán 1838* and *Rico A. 1186*, Yucatán, Mexico, and *Correll 42156*, Bahamas) have at least some flowers that approach *G. polygama* in the disc lobes 1/2 the sepals in length and tapering to a point, or also on occasion the disc lobes 1/2 the sepals in length but not narrowed to a point (e.g., *Zelaya 97*, Honduras, and *von Eggers 6312*, Grenada), or narrowed to a point but 1/3 the length of the sepals (e.g., *Cabrera C. & de Cabrera 9297*, Yucatán, and *Sandoval & Chinchilla P. 762*, El Salvador).

Probable hybrids exist between *Gouania lupuloides* and *G. polygama*, and are discussed under the latter. *Gouania lupuloides* has at times been confused with *G. colombiana*, *G. conzattii*, *G. croatii*, *G. eurycarpa*, *G. guiengolensis*, *G. obamana*, *G. polygama*, *G. rosei*, and *G. stipularis*, and distinguishing characteristics are discussed under those species. Illustrations labeled as *G. lupuloides* but representing other species are found in Krings and Braham (2005: 126, tab. 10.1, fig. C, c, based on *Gentle 236* from Belize [actually *G. eurycarpa*]), Bornstein (1989: 163, tab. 69, fig. a, depicting a flowering branch with most of the leaves having seven or eight lateral veins per side of the midrib [characteristic of *G. polygama*]), Liogier (1982: 62, tab. 13, fig. C, a flower with trichomes along the disc annulus and long apically pointed disc lobes [characteristic of *G. polygama*, a name treated as a synonym of *G. lupuloides* in that publication]).

The name *Gouania lupuloides* has also been misapplied in South America, where it is not known. The specimen cited as this species for Ecuador by Liesner (1999), *Gudiño 527*, MO, I identify as *G. alnifolia* Reissek, which differs from *G. lupuloides* in having relatively longer and lanceolate and acuminate disc lobes and mericarps that are dumbbell-shaped. Two of the specimens cited as *G. lupuloides* for Peru by Macbride (1956), *Klug 2361* and *Méxia 6392*, without herbaria acronyms, I identify (based on the MO duplicates) as *G. riparia* Reissek (following Reissek's original description), which differs in having the floral disc completely pubescent, the

fruits with very thick lobes, the leaves with more lateral veins (ca. eight on either side of the midrib) and the tooth glands with small tufts of trichomes. Two others, *Tessmann 4533* and *4682* (herbaria not indicated), are, based on duplicates of both at G and NY, *G. colombiana* (see that species discussion for distinguishing traits). The specimens cited as *G. lupuloides* by Brako and Pool (1993) for Peru, *Smith et al. 3652* (MO), and by Tortosa (2008) for Argentina, *Vanni 2765* (CTES) and Paraguay, *Zardini 40052* (BAA, MO, PY), are all *G. polygama* (based on the MO duplicates; see discussion below that species for distinguishing traits). The last collection, *Zardini 40052* (G, MO), was additionally cited for *G. lupuloides* in Cusato and Tortosa (2013).

Gouania paniculata Spreng. was published by Sprengel in 1822 as a new species from Hispaniola, included by de Candolle (1825) in his treatment of *Gouania* as *Gouania* ? *paniculata*, and treated by Suessenguth (1953a) as a synonym of *G. lupuloides*. See the Rejected Name section for lectotypification, placement, and discussion.

Selected specimens examined. UNITED STATES. **Florida:** Dade Co.: Miami, *Small & Carter 505* (NY); Elliots Key, *Britton 361* (NY); Monroe Co.: Key Largo, *Correll et al. 40277* (MO); Key West, *Seibert 1231* (MO).

BELIZE. **Cayo:** Branch Mouth N of El Cayo, *Bartlett 11951* (MICH); Chial rd., *Arvigo et al. 733* (MO, NY, US). **Toledo:** Colombia River ca. 1 km from San Pedro, BARC farm, *Houck 3761* (NY). COSTA RICA. **Alajuela:** Zarcero, *Smith A346* (F, MO, NY). **Cartago:** Cerros de La Carpintera, *Lent 3636* (CAS, F, MO, NY, TEX, US). **Guanacaste:** Nicoya, *Tonduz 13786* (BM, GH, K, US). **Puntarenas:** Monteverde, San Luis valley on Pacific slope, *Haber & Bello C. 3532* (MO, TEX); Buenos Aires, R. I. Ujarrás, Cordillera de Talamanca, *Valerio 79* (F, MO); Coto Brus, Z. P. Las Tablas, Cuenca Terraba-Sierpe, camino de Echandi a las Alturas, *Alfaro 1838* (MO). **San José:** Cerros Escazú–La Carpintera, Escazú a Alto Tapezco por Bebedero, *Hammel et al. 19062* (MO, TEX). EL SALVADOR. **Ahuachapán:** San Francisco Menéndez, El Corozo, Mariposario, *Rosales 1519* (BM, MO); San Benito, *Sandoval & Chinchilla P. 762* (MO). **Cabañas:** Cinquera, camp. El Niño, *Monterrosa S. & Carballo 466* (MO). **Chalatenango:** Nueva Concepción, area protegida Pananalapa, El Vado, *King & Chávez 83* (BM, MEXU, MO). **La Libertad:** Finca La Hiralda, *Sidwell et al. 720* (BM, MO). **La Unión:** vic. of La Unión, *Standley 20691* (GH, US). **San Salvador:** San Salvador, *Calderón 1256* (GH, NY, US). **Santa Ana:** lower slopes of Volcán Chingo, *Sidwell et al. 841* (BM, MO, NY). GUATEMALA. **Alta Verapaz:** Cubilgüitz, *von Türckheim 8503* (F, K, NY, US). **Baja Verapaz:** betw. Salamá & Rabinal, *Harmon & Dwyer 4348* (MICH, MO). **Chimaltenango:** Volcán de Acatenango, *Gómez 18* (MO, TEX). **Chiquimula:** Chiquimula, aldea Sabana Grande, *Chávez s.n.* [6 Oct. 1997] (MEXU). **El Progreso:** old rd. near bottom of Río Grande Valley, *Iltis G-67* (F). **Escuintla:** Escuintla, *Morales R. 875* (US). **Guatemala:** near Finca La Aurora, *Aguilar G. 219* (F); near Amatitlán, *Standley 61408* (F). **Huehuetenango:** Nentón, *Seler & Seler 3277* (A, CAS, GH). **Izabal:** Los Amates, *Deam 110* (F, GH, MICH, MO, NY, US). **Jutiapa:** vic. of Jutiapa, *Standley 76326* (F). **Petén:** La Libertad & vic., *Aguilar H. 345* (A, MICH, MO, NY). **Quetzaltenango:** El Palmar, *Skutch 1446* (A, F). **Quiché:** *Aguilar 1127* (F). **Retalhuleu:** region of Ajaxá, E of Santa Cruz Muluá, *Standley 88245* (F). **Sacatepéquez:** 2.3 mi. SW of Alotenango slopes of Volcán del Fuego, *Croat 41935* (MO, TEX). **Santa Rosa:** Cenaguilla, *Heyde & Lux 4127* (G, GH, K, M, US). **Suchitepéquez:** Cocales, *Standley 62079* (F). **Zacapa:** trail betw. Río Hondo & waterfall, *Steyermark 29499* (F). HONDURAS. **Choluteca:** San Marcos de Colón, 7 km N de San Marcos de Colón, *Hazlett 972* (MO). **Comayagua:** along river at Siguatepeque, *Williams & Williams 18471* (F). **Copán:** betw. San Jerónimo & Concepción, Cordillera Gallinero o Grito, *Molina R. et al. 33615* (MEXU, TEX). **Cortés:** along Río Lindo, near Peña Blanca, *Williams & Williams 18809* (F, US). **Francisco Morazán:** Valle de Ángeles, 20 km E de Tegucigalpa, *Zelaya 97* (MO); San Antonio de Oriente, near Jicarito, *Williams & Molina R. 10573* (A, F, LL, MICH, MO). **Lempira:** Gracias, *Nelson et al. 281* (MEXU, MO). **Ocotepeque:** Sinuapa, La Montañita on Cordillera Merendón, *Molina R. 22538* (F, NY). **Olancho:** vic. of Juticalpa, *Standley 17536* (F). **Valle:** Isla Tigre, vic. of Amapala, *Standley 20776* (GH, US). **Yoro:** along Río Guaymón, betw. La Ceiba & San Pedro Sula, *Croat & Hannon 64650* (MO, TEX). MEXICO. **Campeche:** San Antonio Ebulá, *Pavon L. 187* (MEXU); carr. Kalkiní–El Remate, Km. 12.5, *Peña-Chocarro et al. 592* (BM, MEXU, MO). **Chiapas:** Frontera Comalapa, 6 km al W de Cd. Cuauhtémoc, *Soto N. et al. 13493* (BM, MEXU, MO); Villa Corzo, 56 km S of Mexican Hwy. 190 near jct. to Jerico on rd. to Nueva Concordia, *Breedlove & Davidse 54431* (MO; Fig. 1C); 13 km E of Ocozocoautla on Rte. 190, then N on rd. to Aguacera, *Hufi et al. 2259* (BM, MO, TEX); Mirador "Manos que imploran," 10 km al SW de Chicoasén, *Reyes-García & Urquijo 890* (BM, MEXU); Trapichito, near Comitán de Domínguez, *Matuda 5729* (LL, MEXU); Ocosingo, en el vértice del Río Chixoy a 90 km al S de Boca Lacantum, *Martínez S. 18335* (MEXU, MO); a 5 km al E del poblado de Nuevo Guerrero, *Aguilar M. & López A. 9194* (MEXU); 1 km N of Ocozocoautla de Espinosa, *Breedlove 19832* (MO); Pijijiapan, carr. costera Soconusco, *Aquino 211AA* (MEXU); Tapachula, 5 de Febrero, *Ventura V. & López 734* (BM, MO, NY); Tuxtla Chico, La Toma, Soconusco, *Aquino 202AA* (MEXU). **Chihuahua:** Batopilas, *Goldman 218* (F, GH, US); E of La Bufa on side of Barranca de Batopilas, *Bye 8845* (MEXU, MICH); N side of Barranca de Batopilas, betw. La Bufa & Quírare, arroyo Buenas Aires, *Bye et al. 18021* (MEXU). **Durango:** Tabahueto (al catorce), 196 km al W de Tepehuanes, *Torres C. et al. 3560* (F, MEXU, MO; Fig. 1G, NY). **Guerrero:** Chilpancingo, 500 m al N de Rincón de La Via, ca. de la casa de Don Cele, *Kruse 1425* (MEXU, MO); Iguala y Buenavista, Cañón de La Mano, entre Los Amates y El Naranjo, *Catalán H. 184* (MEXU, MO); Malinaltepec, *Wagenbreth 775* (B, MEXU). **Hidalgo:** 22 km W de Huejutla de Reyes, *Hernández M. 4029* (MEXU, MO). **Jalisco:** El Pitillal, 2 km al NE de Puerto Vallarta, *Rzedowski 17801* (MEXU, MICH, TEX); 18–19 km SEE de Autlán, 2–3 km al NE de La Yerbabuena, *Cuevas G. & Nuñez 3987* (MEXU). **México:** Tejupilco, N de Bejucos, S de Nanchititla, *Zepeda G. 279* (MEXU); Temascaltepec, Tenayac, *Hinton 5139* (BM, K). **Michoacán:** Sierra Madre del Sur, ca. 32 km N Playa Azul, *King & Soderstrom 4979* (MEXU, MICH, NY, TEX); Coalcomán, Puerto Zarzamora, *Hinton & Hinton 12248* (K,

MICH). **Morelos:** Llanos de Guarin–Barranca del Terrón, *Vázquez S. 2603* (MEXU). **Nayarit:** 8.5–9.5 km E of Ruiz, *Bartholomew et al. 2606* (GH, MO, NY); lake NE of Santa María del Oro, *Feddema 764* (MICH); Tuxpan, *Mexía 1085* (A, GH, MICH, MO). **Oaxaca:** Tuxtepec, *Martínez Calderón 1601* (MEXU, MO, NY); San Miguel Chimalapa, Rancho Los Domínguez, 4 km al S de Congragación Benito Juárez por el río Portamonedas, *Maya J. 621* (MEXU, MO, NY); Miahuatlán, Mpio. San Jerónimo C., Cañada del Río Trapiches, *Campos V. 3345* (F, MEXU); Pochutla, Mpio. San Miguel del Puerto, San Isidro Chacalapa, *Perret et al. 76* (MEXU, MO); Tuxtepec, Temascal, lado SW de la Presa Miguel Alemán, *Cedillo T. & Torres C. 1036* (MEXU, MO). **Querétaro:** Jalpan, 7–8 km al NW de Rancho Nuevo, *Servín O. 1225* (MEXU). **Quintana Roo:** Cobá, orilla de Laguna de Cobá, *Téllez V. & Cabrera C. 3769* (BM, MEXU, MO, NY). **San Luis Potosí:** Tolosa, *Deam 49* (F, GH, MICH); El Sol, *Sharp 441848* (GH, MEXU); Tamasopo Canyon, *Pringle 3210* (BM, F, GH, K, MEXU, MO, NY, US); Est. For. Exp., 25 km al E de Tamulín, *Rzedowski 23348* (F, LL, MICH). **Sinaloa:** Imala, *Gentry 4949* (GH, MEXU, MICH, MO; Fig. 1E, NY); Estero de Escuinapa, *González Ortega 6113* (GH, MEXU, US). **Tabasco:** 7.58 km al E de Teapa, *Calónico S. et al. 21428* (BM, MEXU, MO); Teapa, Puyacatengo, *Ventura A. 20865* (GH, MEXU, NY). **Tamaulipas:** 10 km NW of El Progresso, 18 km NW of Ocampo, *Stanford et al. 993* (GH, MO, NY); 20 km E de Aldama, carr. a Barra del Tordo, *Martínez 882* (MEXU); 32 km E of Soto La Marina on rd. to La Pesca, *Fryxell 3683* (MEXU, MICH, MO, NY, TEX, US). **Veracruz:** Puente Nacional, Conejos, *Ventura A. 2695* (F, MICH, NY, TEX, US); San Andrés Tuxtla, El Salto de Eyipantla, a 8 km del Pueblo de Sihuapan, *Calzada 1684* (BM, F, MEXU; Fig. 1F); cerros cercanos a Chicuaseu, a 11 km de Actopan, *Lot H. 1050* (BM, F, GH, MO); Zacuapan, *Purpus 2274* (F, GH, MO, NY); Arroyo Blanco 2 km de San Juan del Río brecha a Playa Vicente, *Tenorio L. & Torres C. 5262* (MEXU, MO); Fracionamiento Totonicapan, 3 km al N de Catemaco, carr. Catemaco–Coyame, *Cedillo T. 2913* (MEXU); Jesús Carranza, 3 km del límite con Oaxaca, ca. 37 km al NE de Real de Sarabia, *Perino 3218* (MEXU, NY); Hwy. Mex. 180, 10 km SE of Río Páunco opposite Tampico & 1.5 km NW of Tampico Alto, *Nee & Taylor 28696* (F, NY). **Yucatán:** ruins of Labna, *Darwin 2170 et al.* (MO; Fig. 2H); a 3 km al SE de Tixkokob, 9 km al NO del poblado Ruinas Ake, *Cabrera & de Cabrera 9460* (MEXU, MO; Fig. 1D); alrededores de la zona arqueol. Sayil, a 35 km al SO de Oxkutzcab, *Cabrera C. & de Cabrera 9571* (BM, MO); 3 km al W de Koncal, *Rico A. 1186* (K); Mérida, *Schott 668* (BM, F, MO); carr. Mérida–Sierra Papacal–Chuburná Puerto, 2 km N de Komchen, *Carnevali & May-Pat 5933* (F, MEXU, MO); Celestún, sobre el camino de Chunchucmil, *Durán 1838* (MEXU, MO); Opichén, above Calcehtok, *Darwin 2272* (MO); San Juan Tekax, camino a Iturbide, *Simá 1490* (MEXU); Valladolid, 8 km from Xuilub on rd. to Xocen, *Mogensen 1166* (MO); a 1 km al E de Ticuch, por la carr. Cancún–Valladolid, *Cabrera & de Cabrera 9297* (MEXU, MO, NY). NICARAGUA. **Atlántico Norte:** vic. Waní, *Ortíz 894* (MO, TEX). **Boaco:** 5 km al SE de Camoapa, Tolinapa, *Moreno 18656* (MO, TEX). **Carazo:** Comarca El Aguacate, 4 km S of Jinotepe, *Neill 1053* (MO, TEX). **Chinandega:** 3–4 km al SE de San Pedro de Potrero Grande, Los Laureles, *Moreno 11711* (MO, TEX). **Chontales:** 7.5 km NNE of Cuapa rd. toward Muy Muy, before Matayagual, *Stevens & Montiel J. 28061* (MO). **Estelí:** El Hornillo, S de Santa Cruz, *Moreno 22274* (MO, TEX); Cerro San Ramón, 6.3 km al O de Pueblo Nuevo, *Moreno 5621* (MO, TEX). **Granada:** 1 km al N de Casa Teja, *Moreno 5377* (MO, TEX). **Jinotega:** Valle El Horno, *Moreno 5029* (MO, TEX). **León:** Mpio. de El Sauce, carr. entre el empalme de El Sauce (carr. a San Isidro), *Coronado G. & Rueda 3516* (MO); new rd. from Hwy. 1 (at ca. Km. 135.5 & ca. 10.6 km W of bridge at La Trinidad) to San Nicolás, *Stevens 10246* (MO, TEX). **Madriz:** Finca San Martín, lado N de la casa hacienda, Cerro Volcán Somoto, *Moreno 3004* (MO, TEX). **Managua:** small E-W ridge along Hwy. 8, ca. 0.4 km from Hwy. 2 intersection, *Stevens 5151* (MO, TEX). **Matagalpa:** Puertas Viejas, lado 5 km S de la Laguna Moyuá, *Moreno 4879* (MO, TEX); Hwy. 5, ca. 38.7 km from Hwy. 3 intersection, *Stevens 6030* (MO, TEX). **Nueva Segovia:** 2.8 km. S of Mozonte–San Fernando rd. (at Km. 239) along rd. to San Antonio, *Stevens & Montiel J. 30518* (MO). PANAMA. **Chiriquí:** Jaramillo, E of Boquete, *Schmalzel 1844* (MO); E of Boquete along rd. to Cerro Azul, *Croat 26764* (MEXU, MO).

BAHAMAS. S Bimini, N of airstrip, *Correll 42156* (NY); New Providence, S of Lake Cunningham, *Correll 50213* (NY); Great Abaco Island, ca. 5 mi. N of Dundas Town, main rd., *Wunderlin et al. 8309* (GH, MO). BARBADOS. Foster Hall Wood, *von Eggers 7127* (A). CUBA. **Camaguey:** Cayo Ballenato Grande, *Shafer 916* (NY, US). **Holguin:** Cerro de Fraile prope Holguin, *Ekman 3252 (P.I.T.R. III)* (A). **La Habana:** N of Marianao, *León 5696* (NY, US). **Matanzas:** near Matanzas, *Rugel 1* (BM, MO, NY). **Pinar del Río:** Buenaventura & vic., *Wilson 9450* (NY). DOMINICAN REPUBLIC. **Azua:** jct. Arroyo Hondo & Arroyo Mancebo, new rd. Sabana de Miguel Martín, *Mejía 8332* (MO, NY). **Barahona:** Sierra de Baoruco, 2.6 km desde Las Auyamas de Polo en el camino a Los Charquitos y Las Tayotas, *Zanoni et al. 18969* (MO, NY, TEX). **La Altagracia:** halfway betw. Boca del Yuma town & El Caracol (old bridge over Río Duey), *Zanoni et al. 10737* (MO, NY). **Peravia:** San José de Ocoa, 9 km S of Los Arroyos, near La Horma, *Mejía 8766* (MO, NY, TEX). **Puerto Plata:** Santo Domingo, Cordillera Septentrional, La Cumbre, *Ekman H16102* (G, LL, NY, US). HAITI. **Artibonite:** 18 km NO del Poblado de Gros Morne, en la carr. a Port-de-Paix, *Zanoni et al. 27650* (MO, NY). **Nippes:** Massif de la Hotte, near Etang-Miragoâne, *Ekman H7236* (F, LL, US). **Nord-Quest:** Port-de-Paix, vic. Basse Terre, Tortue Island, *Leonard & Leonard 12451* (US). JAMAICA. **St. Andrew:** Hope River Plain, 1 mi. E of Mona, *Yuncker 17310* (F, MICH, NY). **St. Elizabeth:** near rd. to S coast, *Bretting J-82* (GH, MICH, MO, NY). **St. Thomas:** Four Mile Wood, *Nesbeth & Scott 5* (MO). LEEWARD ISLANDS. **Antigua:** near Fig Tree Hill, *Box 1228* (MO). **Dominica:** St. Mark, Petite Coulibrie, *Whitefoord 5832* (BM). **Guadeloupe:** Carbet, St. Pierre, *Duss 650* (F, GH, MO, NY, PR, US); Basse Terre, ravine de Belou, *Rodriguez 2566* (A). **Marie Galante:** vic. Pointe de Folle Anse, 2 km SW of St. Louis, *Proctor 20297* (A, BM). **Montserrat:** s. loc., *Shafer 321* (F, NY, US). **St. Barthelemy:** St. Jean, *Questel 851* (NY). **St. Maarten:** s. loc., *Boldingh 2811* (NY). PUERTO RICO. rd. to Guilarte Forest, Km. 4.7, *Schubert & Winters 444* (GH, US); Res. For. Guánica, *Boom 10030* (CAS, MO, NY, TEX); San Germán, *Vélez 379* (NY); San Juan, montes de San Patricio, W of Villa Borinquen, *Carrasquillo 117* (NY). VIRGIN ISLANDS. **St. Croix:** Bassin, *Ricksecker 50* (F, MO, NY); Christiansted, *Rose et al. 3606* (US). **St. John:** above Cinnamon Bay on rd. to Herman Farm, *Mori & Woodbury 17003* (NY, TEX). **St. Thomas:** Agric. Exp. Stat.,

Mayagüez Campus, Univ. Puerto Rico, Río Piedras, *Woodbury WI-72* (MO, NY). **Tortola:** Flamingo Pond, *D'Arcy 285* (A). WINDWARD ISLANDS. **Grenada:** s. loc., *von Eggers 6312* (US); Old Fort, *Miller 108* (US); Carriacou, *Howard 10855* (B, BM, GH, MICH, NY). **Martinique:** St. Pierre, *Hahn 373* (G, GH, TEX, US). **St. Lucia:** Soufriere, *Jean-Pierre 51* (A). **St. Vincent:** Lodge Rion, *von Eggers 6832* (A).

10. Gouania obamana A. Pool, sp. nov. TYPE: Mexico. Veracruz. Municipio San Andrés Tuxtla, Estación Biología Tropical Los Tuxtlas, lote 67, selva alta perennifolia, borde, 18°34′–18°36′N, 95°04′–95°09′W, 200 m, 3 abr. 1984, *G. Ibarra Manríquez 1446* (holotype, MEXU!; isotypes, MEXU!, MO!, NY!). Figures 2I, 12A–C.

Diagnosis. New species similar to *Gouania polygama* (Jacq.) Urb., but with mericarps velutinous and with taller wings, larger seeds, and pairs of lateral leaf veins three to five on either side of the blade midrib.

Liana; young branches hollow, abundantly to sparsely tomentose (early glabrescent) or sericeous, trichomes light red-brown. Leaf blades 4.2–13 × 2.3–8 cm, ovate or elliptic, subcoriaceous, adaxial surface drying dark red-brown or black-green, glabrous or with few trichomes restricted to venation, 0.2–0.5 mm, straight, appressed and ascending, white or light red-brown, abaxial surface drying green or light brown-green, when very young sometimes with sparse scattered trichomes, these retained only in axils of venation or sometimes also on venation, 0.1–0.5 mm, ± straight and appressed, on venation ascending, in axils spreading and matted, lateral veins 3 to 5 per side of the midrib, diverging at 45°–60° angles, base rounded to obtuse, or rounded and then shortly decurrent, margin crenulate to nearly entire (rarely crenate with 1.5 to 2 teeth/cm), tooth glands minutely pustular to minutely pulvinate (rarely cupular), apex rounded, acute or obtuse and then bluntly cuspidate or less frequently acute or bluntly acuminate, sometimes apiculate at tip; stipules 2-lobed, lost before leaves expand, upper lobe 3–4 × 0.9–1.5 mm, upward curving to spreading, lanceolate and acuminate, lower lobe 1–2 × 0.4–0.5 mm, downward curving to spreading, lanceolate and acuminate or ovate and acute; petioles 10–25 mm. Inflorescence with longest racemiform part 7–20 cm, indumentum of rachis usually densely tomentose, less frequently minutely puberulent, with trichomes light red-brown to yellow-white, bract of cyme 2–3 mm, lanceolate, acuminate, cymes appearing sessile (rarely with peduncle to 4 mm), mature flowers appearing sessile to pedicels to 1.5 mm, hypanthium densely minutely velutinous with trichomes white-yellow or light red-brown; sepals (0.6–)0.9–1.25 mm, externally abundantly minutely sericeous or tomentose, trichomes white-yellow or light red-brown; petals 0.6–1 mm; stamens with filaments 0.5–0.8(–1) mm, anthers 0.25–0.3 mm; disc excluding lobes 1–2 mm diam., annulus with few to numerous trichomes, disc otherwise glabrous, disc lobes 0.25–0.35 × 0.4–0.6 mm at apex, transversely rectangular to square, generally apically bilobed, 1/4–1/3(1/2) length of sepals; style glabrous. Young fruits densely velutinous, trichomes white-yellow or light red-brown; mature mericarps dumbbell-shaped (Fig. 2I), the wings ± attaching to the base and sides of fruit body, externally drying brown-yellow, darker over fruit body, velutinous with trichomes dense on fruit body and abundant to sparse on wings 0.05–0.5 mm, white or light red-brown, internally drying with wings and fruit body pale yellow or white, or sometimes fruit body slightly darker and/or wings with pale brown radiating indistinct streaks, fruit body 4–6 mm high, wings (9)10–14 mm high, distance between highest points of 2 wings 8–13 mm, width of mericarp 14–20 mm, 2.75–4× height of fruit body, width of fruit body (3–)4–5 mm, 1/5–1/4(–1/3) width of mericarp; seeds ca. 3.5 × (2.6–)2.75–3(3.5) mm, shiny brown.

Etymology. This species is named in honor of Barack Obama, the 44th president of the United States of America, who has stressed the importance of funding basic science.

Phenology. *Gouania obamana* has been collected in flower from December to February and less frequently in March.

Habitat and distribution. *Gouania obamana* is known from Atlantic Mexico in eastern Puebla, Veracruz, and Tabasco and extending across the Isthmus of Tehuantepec into Oaxaca. The species is disjunct in eastern Chiapas extending into Guatemala (Petén and Izabel), Belize, and Honduras (Atlántida). It is found in evergreen forests, from 0 to 950 m elevation (Fig. 4A).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania obamana* is known from 70 collections (58 georeferenced) from Veracruz in Mexico south to Belize and northeastern Honduras, found in evergreen forests. The area of occupancy is estimated to be 172 km^2 and 63% of the collections fall outside of protected areas. Further study is recommended to understand the factors determining this species distribution and any risk factors.

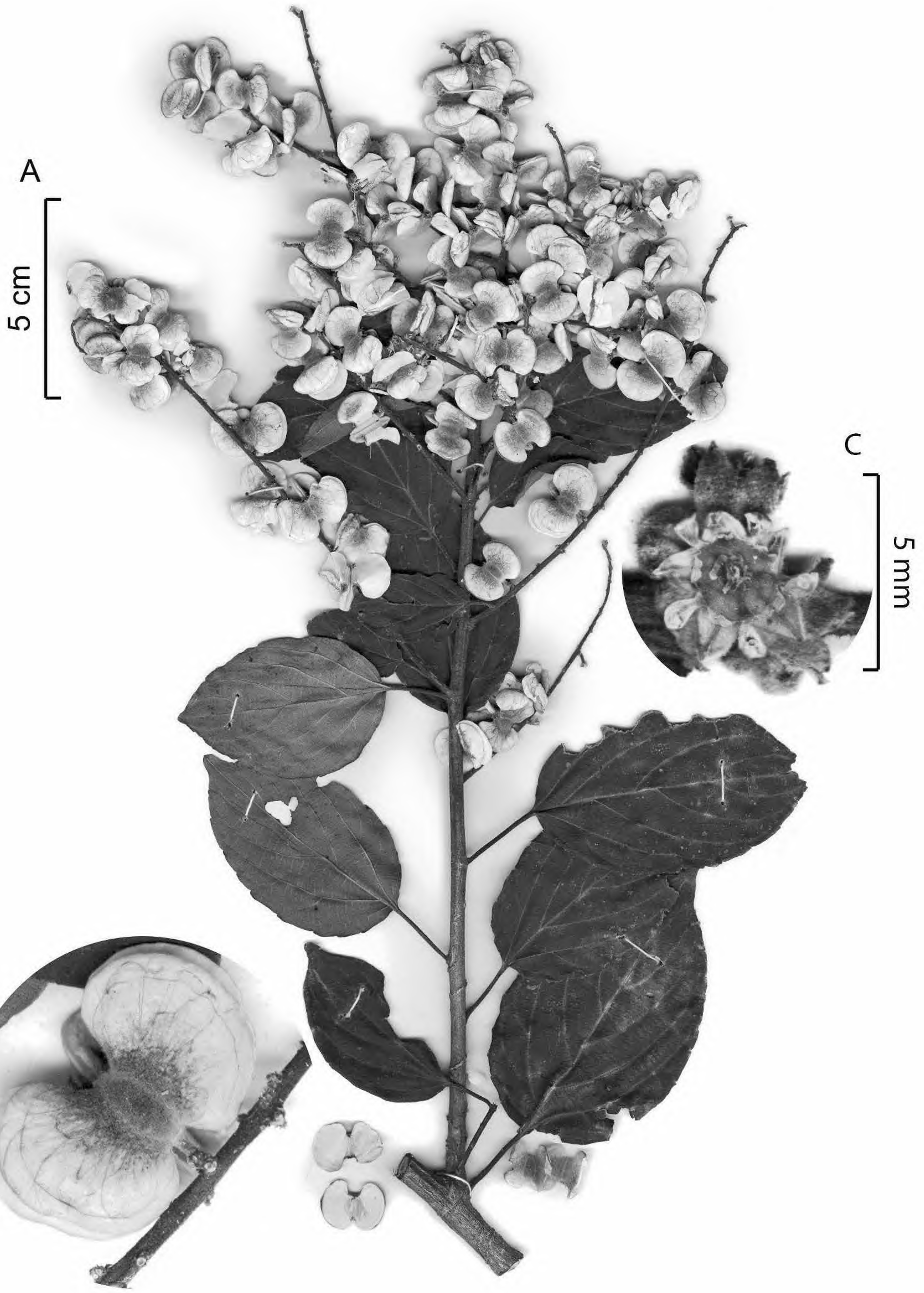


Figure 12. *Gouania obamana* A. Pool. —A. Fruiting branch. —B. Portion of infructescence with fruit. —C. Flower at inflorescence node. A, B scanned from the holotype *G. Ibarra Manríquez 1446* (MEXU); C scanned from the paratype *G. Ibarra Manríquez et al. 5507* (MO).

Discussion. Specimens of this previously undescribed species have been identified and cited in the literature under both *Gouania lupuloides* (for Belize, Balick et al., 2000: *Balick 3612*; *Gentle 1921*, *3185*, *3226*, *8543*, *8641*, *9298*; and for Veracruz, Fernández, 1986: *Calzada 104*; *Dorantes L. et al. 2543*, *3991*; *Ibarra Manríquez 6; Vázquez et al. 16*, *573*; *Ventura A. 12420*, *15039*, *15696*, *18141*) and *G. polygama* (for Veracruz, Fernández, 1986: *Cedillo T. & Calzada 176*; *Dorantes L. et al. 3991*; *Menéndez L.*

91). *Gouania obamana* is similar to *G. polygama* in its dumbbell-shaped fruit and pubescent annulus, but differs in mericarp pubescence and size (velutinous, wings (9)10–14 mm high in *G. obamana* vs. nearly glabrous, wings (4–)5–8(–9) mm high in *G. polygama*), seed size (3.5 mm in *G. obamana*, (1.8–) 2.2–2.75 mm in *G. polygama*), and the number of lateral leaf veins on either side of the blade midrib (three to five in *G. obamana* vs. (six)seven or eight(nine) in *G. polygama*). In addition, the leaves of *G. obamana* are nearly glabrous with tufts of trichomes in the vein axils of the abaxial blade surface, a state not seen in *G. polygama*, and the disc lobes of *G. obamana* are square or transversely rectangular and 1/4–1/3(1/2) the length of the sepals, versus often apically tapering and (1/3–)2/5–3/5(–2/3) the length of the sepals in *G. polygama*. *Gouania obamana* is easily distinguished from *G. lupuloides* by mericarp type and pubescence (dumbbell-shaped and densely pubescent in *G. obamana* vs. butterfly-shaped and glabrous in *G. lupuloides*) and flower annulus (pubescent in *G. obamana* vs. glabrous in *G. lupuloides*). They are also easy to separate when sterile, as *G. obamana* has bicolored, subcoriaceous leaves and the stipules lost very early, while *G. lupuloides* has monocolored, membranaceous leaves and persistent stipules.

One specimen from Chiapas (*Durán F. & Levy T. 360*, MEXU) seems to represent a hybrid between *G. obamana* and *G. polygama*. It has the leaves resembling those of *G. obamana* (subcoriaceous, bicolored, glabrous excluding tufts of trichomes in vein axils, four lateral veins per side of midrib), and the mericarps are pubescent but are much smaller than those of *G. obamana* and fall within the range for *G. polygama* (fruit body height 3 mm, wing height 7 mm, distance between highest points of two wings 6 mm, width of mericarp 9 mm, width of fruit body 3 mm) and seeds only 2.75 mm long.

Paratypes. BELIZE. s. loc., *M. E. Peck 621* (K); Seven Hills, *E. J. F. Campbell 76* (K); Río Grande, *W. A. Schipp 8–457* (F). **Cayo:** Humming Bird Hwy., *P. H. Gentle 8641* (LL, MO, NY, US). **Stann Creek:** Humming Bird Gap, Humming Bird Hwy., *P. H. Gentle 9298* (CAS, LL, MO, NY, US); Stann Creek Valley, Baboon Ridge, *P. H. Gentle 3185* (A, DS, MICH, NY, TEX, US); Mullins River Rd., *P. H. Gentle 1921* (A, F, K, MEXU, MICH, NY), *8543* (CAS, LL, NY); Stann Creek Valley, Antelope Ridge, *P. H. Gentle 3226* (A, MICH, NY). **Toledo:** rd. to Laguna Village off hwy. from Dangriga to Punta Gorda, *M. J. Balick et al. 3612* (MO, NY, US); betw. Rancho Chico & Cockscomb, Monkey River, *P. H. Gentle 4376* (MICH, TEX); near Jacinto Hill, *P. H. Gentle 5121* (LL, MO). GUATEMALA. **Izabal:** Río Chacón, *H. Johnson 1194* (F); Entre Ríos, *H. E. Kuylen "E"* (US); near Entre Ríos, *P. C. Standley 72684* (F); betw. Cienaga & Puerto Méndez, along Petén–Río Dulce Hwy., *R. Tún Ortíz 2354* (BM, F, MICH); 1.4 km N of San Felipe, *W. E. Harmon & J. A. Fuentes 2082* (MEXU, MO); El Estor, *E. Contreras 11148* (CAS, LL, MO); Morales, *W. A. Kellerman s.n.* [8 Mar. 1907] (US); Puerto Barrios, *C. C. Deam 68* (GH, MICH), Puerto Barrios, ca. 20 km from town on rd. to Machacas, *N. T. Marshall et al. 319* (TEX). **Petén:** Flores–Poptún Rd., Km. 85, *C. L. Lundell 17312* (CAS, F, LL, US); San Pedro, Km. 160 Cadenas Rd., *E. Contreras 9498* (LL, MO, US); Los Arcos, W of Km. 149 Cadenas Rd., *E. Contreras 9450* (LL, MO, NY, US). HONDURAS. **Atlántida:** Cuyamel, *M. A. Carleton 442* (US). MEXICO. **Chiapas:** Ocosingo, en el vertice del Río Chixoy camino a Chajul, sobre la carr. fronteriza del S, *E. M. Martínez S. M-16082* (MO), en Nv. Chihuahua a 28 km al N del vertice del Río Chixoy camino a Boca Lacantum, *E. M. Martínez S. 16181* (MO), a 2 km al N de El Turrbo camino Monte Líbano Chancala, *E. M. Martínez S. 17454* (MO), en Ejido Loma Bonita, *E. M. Martínez S. & R. Lombera 26087* (K, MEXU). **Oaxaca:** Comaltepec, Puerto Eligio, Km. 152 carr. Tuxtepec–Oaxaca, Sierra Juárez, *G. Martínez Calderón 710* (F, TEX); Juchitán, 12 km al N de Guevea de Humboldt, *R. Torres C. et al. 2539* (MEXU, MO, NY); Tehuantepec, Belleville, *C. R. Orcutt 3048* (DS, F, MO). **Puebla:** Hueytamalco, Campo Experimental "Las Margaritas," Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, *G. Ibarra Manríquez et al. 5507* (MO), *G. Ibarra Manríquez et al. 5546* (MEXU, MO). **Tabasco:** 37 km al E de Francisco Rueda, carr. a Huimanguillo, *R. Fernández 2351* (NY); Huimanguillo, camino al Ejido Carlos A. Madrazo, *M. de la A. Guadarrama O. et al. 6106* (MEXU). **Veracruz:** Dos Ríos, *C. D. Mell 505* (F, NY, US); Cerro de San Martín, *J. I. Calzada 104* (F, LL, MEXU); Fortuño, Coatzacoalcos River, *L. Williams 8451* (F, US); Catemaco, Laguna de Sontecomapan, Frente al Río la Palma, *F. Menéndez L. 91* (F, MEXU, MO), Sierra Santa Martha, 14 km SE de la desviación hacia el Batonal, *G. Ibarra Manríquez 6* (MEXU), 30 km al E de Tebanca en Las Cumbres del Poblado el Bastonal, *R. Cedillo T. & J. I. Calzada 176* (F, MEXU, NY); Coatzacoalcos, a 0.5 km al S de los officina de la Comisión Nacional del Agua, *C. H. Ramos Á. & E. M. Martínez S. 2253* (MEXU); Hidalgotitlán, 6 km E de Cedillo camino a La Laguna, *J. Dorantes L. et al. 2543* (F, MEXU, MO), *3991* (MEXU), Brecha Hnos. Cedillo–La Escuadra, *M. Vázquez 573* (F, MEXU), *M. Vázquez et al. 16* (MEXU, MO); Jesús Carranza, al S de Pob. 2 en nuevo camino a Ejido La Paz, *T. L. Wendt & H. Hernández G. 5635* (MEXU); San Andrés Tuxtla, 32 km al N de Catemaco camino a Montepio, *R. Cedillo T. 2624* (F, MEXU), Ejido Balzapote, 2.5 km N de la Est. Biol. Trop. Los Tuxtlas, *S. Sinaca C. 1357* (MEXU), Montepio, 40 km NE del camino Catemaco–Montepio, *G. Ibarra Manríquez 30* (MEXU, MO); San Andrés Tuxtla, Est. Biol. Trop. Los Tuxtlas, *T. P. Ramamoorthy 3382* (MEXU), *C. León G. & A. Campos V. 22* (MEXU), lote 67, *A. Campos V. 5236* (MEXU), *G. Ibarra Manríquez 30a* (MEXU), *421* (MEXU, MO), *G. Ibarra Manríquez & S. Sinaca C. 1251* (MEXU), Laguna Zacatal, *G. Ibarra Manríquez & S. Sinaca C. 3340* (MEXU, MO), Cerro Vigía, *G. Ibarra Manríquez & S. Sinaca C. 3084* (MEXU, MO; Fig. 2I), camino a la Laguna Escondida, *M. O. Dillon et al. 1845* (F, NY, TEX); Tlapacoyan, Cuauhtojapan, *F. Ventura A. 15696* (MEXU), Las Ventanas, *F. Ventura A. 15039* (MEXU), El Limón, *F. Ventura A. 18141* (MEXU), El Papatal, *F. Ventura A. 12420* (MEXU, MICH).

11. Gouania polygama (Jacq.) Urb., Symb. Antill. 4: 378. 1910. Basionym: *Rhamnus polygama*

Jacq., Enum. Syst. Pl. 17. 1760. *Gouania tomentosa* Jacq., Select. Stirp. Amer. Hist. 263. 1763. *Lupulus lupuloides* var. *tomentosus* (Jacq.) Kuntze, Revis. Gen. Pl. 1: 119. 1891. TYPE: s. loc., s.d., "*Herbar. Dr. Jacquin*" *s.n.* (lectotype, designated here, BM1030555!). EPITYPE: Haiti. Banks of Jean Rabel River betw. Bord de Mer & Jean Rabel, 30 Jan. 1929, *E. C. Leonard & G. M. Leonard 12661* (epitype, designated here, US!; isoepitypes, A!, NY!). Figure 2J.

Gouania pubescens Poir. var. *pubescens*, Encycl., Suppl. 2: 819. 1811 [1812]. *Lupulus lupuloides* var. *pubescens* (Poir.) Kuntze, Revis. Gen. Pl. 1: 119. 1891. TYPE: [Haiti] Saint-Domingue, Herb. Lamarck (lectotype, designated here, P-LA not seen, microfiche LM 131/12!).

Gouania crenata var. *cordifolia* DC., Prodr. 2: 39. 1825. TYPE: [Dominican Republic.] Sancto-Domingo, s.d., *C. L. G. Bertero s.n.* (holotype, G-DC not seen, digital image!).

Gouania virgata Reissek in Mart., Fl. Bras. 11(1): 104, tab. 37. 1861, syn. nov. *Gouania virgata* Reissek var. *virgata*, as "[var.] β. *guianensis*" Reissek in Mart., Fl. Bras. 11(1): 105. 1861. TYPE: [Guyana.] "Guyanae britanicae interioris," June 1839, *R. H. Schomburgk 584* (lectotype, designated here, W-0031735 not seen, digital image!; isolectotypes, BM-956387 [date 1838]!, digital image!, BM-544362 [date 1838] not seen, digital image!, BR [s.d.] not seen, digital image!, F [s.d.]!, K [labeled "1st coll."]!, K [date 1838]!, L [s.d.] not seen, digital image!).

Gouania virgata var. *brasiliensis* Reissek in Mart., Fl. Bras. 11(1): 105. 1861, as "[var.] α. *brasiliensis*," syn. nov. TYPE: Brazil. [Minas Gerais] "Barra das Velhas ad ripas fluv. Rio de S. Francisco in prov. Minarum," *J. B. E. Pohl 731 (3107)* (lectotype, designated here, W-0031733 not seen, digital image!, F-neg. 32604!, W lecto. fragm. at F!; isolectotypes, K not seen, digital image!, W-0031734 not seen, digital image!).

Gouania mexicana Sessé & Moc., Fl. Mex., ed. 2, 236. 1894, syn. nov. TYPE: [Mexico?] "calidis N. H.," [Nueva Hispania] *M. Sessé, J. M. Mociño, J. D. del Castillo & J. Maldonado 5202* (lectotype, designated here, MA not seen, F-neg. 47631 [collection # of Field Museum photo label in error 5200]!, digital image!; MA lecto. fragm. at F!).

Liana; young branches solid, indumentum abundantly to densely villous or velutinous (less frequently pilose or tomentose), trichomes red-brown to light red-brown (less frequently yellow). Leaf blades 4–11(–15) × 2–7(–9.5) cm, elliptic, less frequently widely elliptic, ovate, or oblanceolate, membranaceous, adaxial surface drying dark green, or less frequently, dark red-brown, black-green, brown-green (rarely green), glabrous to less frequently abundantly pubescent, with trichomes 0.2–1 mm, straight to slightly curved, most frequently all ascending, sometimes spreading in all directions or kinky, yellow-white to red-brown, abaxial surface drying yellow-green (rarely green and same color as adaxial surface), usually abundantly to densely pubescent, rarely nearly glabrous with trichomes 0.2–1 mm, kinky or straight to slightly curving and spreading in all directions overall or sometimes trichomes of venation straight to slightly curving and mostly ascending, white-yellow to red-brown, lateral veins (6)7 or 8(9) per side of the midrib, diverging at 45°–60° angles, base subcordate, rounded, or cordate, frequently then shortly decurrent, margin serrulate to nearly entire, crenate or serrate, 1 to 4 teeth/cm, tooth glands pustular to cupular, apex acuminate or acute to obtuse and then often cuspidate; stipules 2-lobed, caducous, usually present only at the base of unexpanded leaves or very young leaves, or on juvenile plants, upper lobe (1.5–)2.5–7(–8) × 0.4–2(–3) mm, spreading upward to downward (rarely erect), lanceolate, sometimes asymmetrically so, acuminate (rarely acute), lower lobe (0.5–)1–3.5(–4) × 0.25–1.25 mm, curving downward, less frequently spreading, ovate to lanceolate, acute to acuminate (rarely oblong and acute or subulate foot); petioles (3–)4–15(–22) mm. Inflorescence with longest racemiform part (7–)11–32(–42) cm, rachis villous, velutinous, or tomentose with trichomes yellow-white to red-brown, bract of cyme (1–)1.5–3 mm, lanceolate, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 1.5(–2.5) mm, hypanthium and sepals externally densely to abundantly sericeous to tomentose with trichomes yellow-white or light red-brown; sepals (0.5–)0.65–1(–1.2) mm; petals (0.5–)0.6–0.9(–1) mm; stamens with filaments (0.35–)0.5–0.75(–0.8) mm, anthers 0.15–0.25(–0.3) mm; disc excluding lobes (0.9–)1–1.5(–1.8) mm diam., annulus with few to numerous trichomes, disc otherwise glabrous, disc lobes (0.25–)0.3–0.5(–0.6) mm, often lanceolate, acuminate or tapering, less frequently ± square and to 0.4 mm at apex, apically entire or irregularly lobed, (1/3–)2/5–3/5(–2/3) length of sepals; style pubescent. Young fruits sparsely (rarely abundantly) pilose, trichomes yellow-white to red-brown; mature mericarps dumbbell-shaped (Fig. 2J), the wings ± attaching to the sides of fruit body only, externally wings drying brown-yellow, yellow-brown, or red-brown, fruit body usually drying darker, brown, red-brown or black, glabrous to trichomes sparse on fruit body and sometimes wings with some trichomes 0.1–0.3 mm, yellow-white to red-brown, internally drying yellow-white or off-white on wings, slightly to moderately contrasting with fruit body pale brown, pale red-brown, or pale gray-brown, fruit body (2.5–)3–4 mm high, wings (4–)5–8(–9) mm high, distance between highest points of 2 wings (5–)6–10(–13)

mm, width of mericarp (7–)9–17 mm, 3–4(–5) × height of fruit body, width of fruit body (2–)2.5–3.5(–4) mm, 1/6–1/4(–1/3) width of mericarp; seeds (1.8–)2.2–2.75 × 1.4–2.3 mm, green-brown to brown.

Iconography. Gaertner (1805: tab. 183, fig. 1, as *Gouania tomentosa*); Reissek (1861: tab. 25, fig. 8 and tab. 37, as *G. virgata*); Nowicke (1971: 282, tab. 8, as *G. lupuloides*); Liogier (1982: 62, tab. 13, fig. C, as *G. lupuloides*); Fernández (1986: 33, tab. 5); Acevedo-Rodríguez (2003: 364, tab. 144, fig. I–N); Lima and Giulietti (2005: 334, tab. 1, fig. I–J, as *G. virgata*); Krings and Braham (2005: 126, tab. 10.1, fig. D); Cusato and Tortosa (2013: 25, tab. 7, fig. A, C, as *G. lupuloides*).

Habitat and distribution. *Gouania polygama* is known from Mexico (Oaxaca and San Luis Potosí to Chiapas and Campeche), Guatemala (excluding much of the central highlands), Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Cuba, Hispaniola, Puerto Rico, St. Vincent, Grenada, Tobago, Trinidad, Colombia, Venezuela, Guyana, Brazil, Ecuador, Peru, Bolivia, Paraguay, and the northeastern tip of Argentina. It is found in a variety of vegetation types, but most frequently in evergreen or sub-evergreen forest, also occasionally in oak forest, pine forest, elfin forest, cloud forest, and dry forest, and from 0 to 1200 (rarely to 1800) m in Mexico, Central America, and the West Indies, but most commonly at 0–500 m in elevation (Figs. 4B, 7B, 8B).

IUCN Red List category. Assessed as Least Concern (LC) by IUCN (2012) criteria, *Gouania polygama* is very common in a variety of habitats from Mexico to Argentina and the West Indies.

Phenology. In Mexico, Belize, Guatemala, Honduras, and El Salvador, *Gouania polygama* has been collected in flower from September to November (rarely December to March, June, and August). In Nicaragua, Costa Rica, and Panama, flowering is known from October to February (rarely March, April, June, and September); in the West Indies, flowering is recorded from September to December (rarely January, March to June, and August).

Discussion. Most modern floras (Standley, 1923; Standley & Steyermark, 1949; Liogier, 1953b; Fernández, 1986, 1996; Johnston, 2001; Acevedo-Rodríguez, 2003) have separated *Gouania polygama* from *G. lupuloides* primarily on leaf pubescence. However, while throughout most of its range *G. polygama* tends to have the abaxial leaf surface covered with numerous spreading or kinky trichomes, and *G. lupuloides* tends to have the abaxial leaf surface with few appressed trichomes restricted to the venation, there are numerous exceptions. This has resulted in taxonomic confusion, misapplication of names, and the lack of recognition of additional species or, alternatively, the placement of *G. polygama* in synonymy below an extremely variable *G. lupuloides* (Nowicke, 1971; Liogier, 1982). Careful typification of these early names is of critical importance for their clear applications.

Jacquin (1760) published two species of *Rhamnus* without indication of types and with identical short descriptions, except that *R. polygama* was described as having tomentose leaves and *R. domingensis* as having glabrous leaves. The same author later (Jacquin, 1763) published the new genus, *Gouania*, with two species (*G. tomentosa* and *G. glabra*), explaining that they had been previously treated in *Rhamnus* (Jacquin, 1760); the one described with tomentose leaves, *G. tomentosa*, is equivalent to (but not superfluous for) *R. polygama*, as the name *R. polygama* was not explicitly cited in Jacquin (1763) (Art. 52.2, McNeill et al., 2012). The locality of both was indicated as "Domingensibus" (Jacquin, 1763: 264), and the species descriptions are not particularly helpful in distinguishing the two species or in fixing the application of the names. However, the genus description is clearly based on the first species, *G. tomentosa* (see discussion of derivation of genus name, above), with details (laciniate division of the disc and sub-rounded mericarp wings) that pertain, for the species found in Hispaniola, only to *G. polygama/tomentosa*. *Gouania glabra* is illustrated in a plate, but no illustration was provided for *G. tomentosa*.

In my search through the literature (Smith, 1819 [1811]; de Candolle, 1825; Reissek, 1861; Urban, 1921), I have found no reference to anyone actually having seen type material of *Rhamnus polygama/Gouania tomentosa*, and Bornstein (1989) indicated that type material was doubtfully preserved. I have seen only one specimen of *Gouania* from Jacquin's herbarium (BM-1030555). There is no indication of where it was collected, and the only writing on the front of the sheet is in pencil "*Gouania tomentosa* Jacq. Amer." and the number "11" (probably neither in Jacquin's hand). The back of the sheet is labeled in ink "Herbar. Dr. Jacquin." The specimen, consisting of one leaf with eight lateral veins on the left side of the midrib and seven on the right, is consistent with *G. polygama*, but inconsistent with *G. lupuloides* (lateral veins four or five, rarely three or six, per side of the blade midrib). If I knew that the

specimen had been collected in the West Indies, or that the only *Gouania* species in Jacquin's herbarium were *G. polygama* and *G. lupuloides*, I could state with little doubt that this is authentic material of *R. polygama*. As I cannot absolutely verify this, the sheet chosen as the lectotype of *R. polygama* (and *G. tomentosa*) is designated with reservations and an epitype is indicated. While "Domingensibus" (Jacquin, 1763: 264) could refer to either Haiti or the Dominican Republic, Jacquin seems to have collected only in Haiti (following Howard, 1973: 439, in Cap Français, Jacquesi, Leogane, Port au Prince, and Bayaha [an earlier name for Fort Liberté]). I have therefore selected as the epitype of *R. polygama* and *G. tomentosa* a fruiting collection from Haiti, *E. C. Leonard & G. M. Leonard 12661* (US), with duplicates at A and NY. The specimens are in agreement with the descriptions of Jacquin for *R. polygama* and *G. tomentosa*, and the older leaves match closely those of the lectotype. The fruits also match the plate in Gaertner of *G. tomentosa* (1805: tab. 183, fig. 1) cited by de Candolle (1825) and further provide consistency in the usage of the names. This follows the usage of those authors (Bornstein, 1989; Liogier, 1994; Krings & Braham, 2005) who have placed emphasis on mericarp shape and the presence of trichomes along the disc annulus, as retained on some fruits of the epitype.

There is a sheet (BM-956391) of *Gouania polygama* annotated by Maarten Christenhusz, 2008 "ex Herb. Jacquin, Type of *Gouania tomentosa* Jacq.," which bears two separate collections. The smaller one is labeled "St. Domingue" and consists of one leaf and a number of broken very young fruits, while the other specimen (which seems to be associated with the Christenhusz annotation) is much larger with numerous leaves and flowers in bud. The label indicates that it was collected around "Du Cap" and refers to a communication from Pavon upon the use of this species in Peru. This comment would date at least the label to, at the earliest, 1777 (after publication of both *Rhamnus polygama* and *G. tomentosa*). I have seen only an image of this herbarium sheet, but Jonathan Gregson, Collections Manager of Flowering Plants at BM, has informed me that there is nothing on either the front or back of the sheet to indicate that it was ever part of Jacquin's herbarium, and I cannot find a way to justify treating either of the specimens as authentic material of *R. polygama/G. tomentosa*.

Lamarck (1789: 5) published the name *Gouania crenata* Lam. as questionably separate from *G. tomentosa*, but with somewhat less pubescent leaves than those described by Jacquin. The description is strictly vegetative, as is the specimen presumed to be the holotype (the only collection labeled *G. crenata* at P-LA not seen, digital image!, with no other information on the label). There is nothing in the description or the image of the presumed type that would suggest this is not *G. polygama*. However, without any fertile material, and without knowing where it was collected (in protologue, Lamarck, 1789: 5, as "Amérique méridonale"), this name remains in doubt. De Candolle (1825) published *G. crenata* var. *cordifolia* based on *C. L. G. Bertero s.n.*, St. Domingo, a specimen that consists of two leaves, a tendril, and a small twig. I have seen an image of this and, as the leaf has seven lateral veins per side of the midrib, place it in synonymy of *G. polygama* (following Urban, 1921, and Suessenguth, 1953a).

Poiret (1811 [1812]) published *Gouania pubescens* with two varieties. For *G. pubescens* var. *pubescens*, he provided a description of a plant in flower and cited a specimen from Saint-Domingue (at Herb. Lamarck) and a plate in Lamarck, 1799 (t. 845, f. 1). I have chosen this specimen, of which I have seen a microfiche, as the lectotype. The flowering branch and magnified images of the flower in the Lamarck plate also pertain to the type variety. See the discussion of *G. lupuloides* regarding the placement of *G. pubescens* var. *martinicensis*. I place *G. pubescens* var. *pubescens* in synonymy of *G. polygama* (following Urban, 1921, and Suessenguth, 1953a).

Grisebach published the name *Gouania tomentosa* var. *pubescens* in 1860, without description, citing only the collection number, *C. Wright 75*, and while invalidly published, this name is sometimes seen in the literature and on herbarium specimens. I have seen a number of *C. Wright 75* sheets with various collection dates (Jan. 1859–July 1859; Sep. 1859–Jan. 1860; Sep. 1860; 1861), which are *G. polygama* and one sheet dated 1865 (after the publication of *G. tomentosa* var. *pubescens*), which is *G. lupuloides*.

Reissek (1861) published *Gouania virgata* with four syntypes (*R. H. Schomburgk 584* and *711* from Guyana, *E. R. Friedrichsthal*, without collection number, from Nicaragua, and *J. B. E. Pohl*, without collection number, from Brazil) and two varieties (*G. virgata* var. *brasiliensis*, with the adaxial leaf surface densely pubescent, and *G. virgata* var. *guianensis*, with the adaxial leaf surface sparsely pubescent), without indication of which syntypes pertained to which variety. He also cited the first publication of the name *G. virgata* as a nomen nudum from Guyana, in Schomburgk (1848 [1849]). From the latter it is assumed that the variety published as *G. virgata* var. *guianensis* is the type variety (*G. virgata* var. *virgata*) and that the lectotype for the species should be

selected from one of the Guyana collections. M. C. Johnston, in 1969, annotated the W-0031729 sheet of *R. H. Schomburgk 711* (Roraima, 1842–1843) as the lectotype of *G. virgata* var. *guianensis*. I have searched through the literature but have been unable to find publication of the lectotypification. I cannot follow Johnston's annotation, because there is no indication that Reissek ever saw this collection. It bears neither his annotation nor one of his illustrations. The same is true for the other material of *R. H. Schomburgk 711* that I have observed: BM (Roraima, 1842–1843, digital image!), K (1844)!, digital image!, G (Roraima, 1842–1843), F-neg. 23295!, digital image!, W-1889-0198876 (Roraima, 1842–1843), digital image!. The only material that I have seen from Guyana that is annotated as *G. virgata* in Reissek's hand is *R. H. Schomburgk 584* (collected June 1839), W-0031735 (digital image!), and this specimen is therefore selected as the lectotype. The other syntype of *G. virgata* var. (*guianensis*) *virgata* is *Friedrichsthal 646* (collected in Nicaragua in 1839, W-0031732!). It is clear that this sheet was studied by Reissek (and is therefore a syntype), as it bears his illustration and annotation. Two duplicates of this specimen (without collection number and without annotation in Reissek's hand) are also at W (W-0031730, digital image!, and W-0031731, digital image!). In addition to the presumed isosyntype *R. H. Schomburgk 711* (K) and the excellent illustration of the syntype *Friedrichsthal 646*, I have studied four actual specimens labeled *Schomburgk 584*, which are assumed to be duplicates of the lectotype; however, two have the date 1838 (BM-956387 and K), and two have no dates (F, K). This study, in addition to the examination of the digital image of the lectotype at W, supports placement of this name in synonymy of *G. polygama*.

The *Pohl* collection is most appropriately selected as the type of *Gouania virgata* var. *brasiliensis* as it is the only collection in the protologue cited from Brazil. Reissek (1861: 105) did not provide a collection number for the *Pohl* specimen in the protologue. However, he did cite the locality (as "Barra das Velhas ad ripas fluv. Rio de S. Francisco in prov. Minarum"), and I have seen a photo at F of a *Pohl* collection at W, and the digital image of the same (W-0041733), with the numbers *731* and *3107* with similar locality, "Barra das Velhas," and annotated in Reissek's handwriting, "*Gouania virgata* Reiss. β *brasiliensis*." Therefore, the *Pohl* specimen is chosen as the lectotype. One small deviation from the protologue is that variety *brasiliensis* was published as the α variety. The F sheet with the photo also has attached a large fragment from the W sheet. A digital image of a *Pohl* specimen at K with the number *731* and same locality, but not annotated by Reissek, was also observed. The W sheet of *J. B. E. Pohl 731(3107)* can safely be assumed to be the basis of *G. virgata* var. *brasiliensis*, and is selected as the lectotype. My examination of the fragment at F clearly supports placement of this name in synonymy of *G. polygama*.

As the focus of this paper is Mexico, Central America, and the Caribbean region, I have not attempted to provide a complete list of synonyms beyond that range; the *Gouania virgata* varietal names are included because of the citation of a syntype from Nicaragua. *Gouania virgata* is treated as an accepted species in the recent literature, including Berry and Steyermark (2007), Lima (2010), Boggan et al. (1997), Lima and Giulietti (2005), and Tortosa (1995). Escalante (1946) recognized both *G. virgata* and *G. polygama* (as *G. tomentosa*). However, the latter name must be misapplied, as it was characterized in the key with having a completely glabrous disc and was described as having a pubescent fruit. In addition, Escalante cited Jacquin, 1763: tab. 179, fig. 40, as this species, while Jacquin cited this for *G. glabra*. Tortosa (2008) placed *G. virgata* in synonymy under *G. lupuloides*.

Gouania mexicana was published by Sessé and Mociño in 1894, with a note at the end of the description indicating that Sessé and Mociño had originally (1887 [1888]) treated *Phylica scandens* Sessé & Moc. (see synonomy of *G. stipularis*) as including both a glabrous and tomentose form, with the tomentose form now (1894) being recognized as *G. mexicana* and the glabrous form as *G. domingensis* (see discussion under *G. stipularis*). McVaugh (2000) found two specimens (*3806* and *5202*) in the Sessé and Mociño herbarium at MA with the original label of *G. domingensis*, but no specimens with original labels of *P. scandens* or *G. mexicana*. I have seen F duplicates of both *3806* (in bud) and *5202* (in fruit), as well as the photos of the two sheets at MA and a digital image of *5202* (at MA). The specimens match the description of *G. mexicana*, and I consider the MA sheets of both to be authentic material of *G. mexicana*. The label of *G. domingensis* is not contradictory to this, given the history of Sessé and Mociño's treatment of these species. The F sheets of both are without doubt taxonomically recognizable as *G. polygama*. I select the MA sheet of the fruiting specimen (*5202*) as the lectotype of *G. mexicana*, as it can be identified with greater certainty from the photo (and digital image) than the specimen in bud, and place *G. mexicana* in synonymy under *G. polygama*. *Gouania mexicana* has been previously treated as a

synonym of *G. stipularis* (Standley, 1923; Sussenguth, 1953a, Fernández, 1986), which would be at odds with my selection of the lectotype. However, the placement of *G. mexicana* below *G. stipularis* to me seems unjustified, as *G. stipularis* consistently has glabrous or nearly glabrous leaves, whereas Sessé and Mociño described the abaxial leaf surface of *G. mexicana* as tomentose. The most remarkable feature of *G. stipularis* are its stipules, which Sessé and Mociño described for *P. scandens* and *G. domingensis* (sensu Sessé & Mociño, 1894), but not for *G. mexicana*. Both *3806* and *5202* have lost their stipules, as is usually the case in *G. polygama*. It should be noted that *Sessé & Mociño 5202b*, of which I have seen a digital image from MA and a duplicate at F, is a collection of *G. lupuloides* in flower. Neither specimen of *5202b* had any original label information or determination from Sessé and Mociño.

In North America, *Gouania polygama* in fruit is almost always very easy to recognize due to its small, nearly glabrous, dumbbell-shaped mericarps. However, the mericarps can on occasion be somewhat more pubescent with some trichomes found on the wings, as found on *Johnston 619* collected on San José Island in the Gulf of Panama. Most plants from South America with nearly glabrous, dumbbell-shaped mericarps are *G. polygama*, but there is another species, *G. alnifolia* Reissek, from Putumayo Department, Colombia (e.g., *Etienne s.n.*, CAS), eastern Ecuador (e.g., *Gudiño 532*, MO), Pando, Bolivia (e.g., *Jardim 1029*, MO), Rondônia Territory, Brazil (e.g., *Prance et al. 6238*, MO), and throughout Amazonian Peru (e.g., *Gentry 43562*, MO), which has similar shaped, glabrous mericarps. *Gouania alnifolia* differs in having very distinctive red rays on the inner surface of the mericarp wings and lacks trichomes along the disk annulus.

As previously mentioned, most modern floras have separated *Gouania polygama* from *G. lupuloides* primarily on leaf pubescence. Throughout most of its geographic range in Mexico, Central America, and the West Indies, specimens of *G. polygama* have leaves with the abaxial surface densely pubescent. However, abaxial leaf surfaces that are nearly glabrous, or with trichomes restricted to the venation, are typical from material on the Osa Peninsula of Costa Rica and in Panama in Colón, San Blas, Darién (excluding inlets on coast), Barro Colorado Island, and the southern part of the former Canal Zone. Leaf pubescence is more variable in the South American material. *Gouania lupuloides* can have the abaxial surface of the leaves varying from densely pubescent to glabrescent. In fact, in central Guatemala above 1000 m, the abaxial leaf surfaces of specimens of *G. lupuloides* are nearly always densely pubescent. *Gouania lupuloides* differs from *G. polygama* in having a glabrous disc annulus, disc lobes 1/5–2/5(1/2) the length of the sepals and butterfly-shaped mericarps. Sterile specimens can often be recognized based on the number of lateral veins and stipule retention: (three)four to six veins per side of the blade midrib and the stipules persistent in *G. lupuloides* versus (six)seven or eight(nine) lateral veins on either side of the midrib and the stipules caducous in *G. polygama*.

I have seen one collection from Veracruz, Mexico (*Purpus 15305*, F, GH), that is almost certainly a hybrid between *G. polygama* and *G. lupuloides*. It has in common with *G. lupuloides* the characteristics of leaves with four and five lateral veins per side of the midrib, retained stipules, and disc lobes as wide to twice as wide as long and 1/3 to 1/2 the length of the sepals; the *Purpus* collection shares with *G. polygama* its sessile flowers and the annulus with numerous trichomes. Three collections from Ixtapa, Chiapas (*Breedlove 11876*, F, LL, NY; *Laughlin 1625*, LL; and *Ton* [= *A. Méndez Girón*] *3355*, F, LL, MICH, MO, NY), are also probable hybrids of *G. polygama* and *G. lupuloides*. The three collections have in common with *G. lupuloides* the retained stipules, with the lower lobe wide oblong or reniform, but differ in the leaves with six and seven lateral veins per side of the midrib, as seen in *G. polygama*. The first two are mainly in bud, but have a few flowers; the disc lobes are similar to those of *G. lupuloides* in size and shape (ca. 1/3 sepal length and wider than long) but have a few trichomes along the annulus as in *G. polygama*). The last collection has nearly mature mericarps shaped like those of *G. lupuloides*. One flowering collection from the Dominican Republic (*Mejía & Pimentel B. 17293*, MO, NY, TEX) might also be a hybrid between *G. lupuloides* and *G. polygama*; it resembles *G. lupuloides* in all respects except for having trichomes along the disc annulus.

The name *Gouania polygama* has been frequently misapplied to all *Gouania* species (in Mexico, Central America, and the West Indies) that may have pubescent leaves, which would include *G. conzattii*, *G. croatii*, *G. ekmanii*, *G. eurycarpa*, *G. ferruginea*, *G. guiengolensis*, *G. pubidisca*, *G. rosei*, and *G. velutina*. See discussions under these species for the particular traits that can be used to separate them from *G. polygama*. The name *G. polygama* has also been misapplied to specimens of *G. obamana*, despite its nearly glabrous leaves (cf. discussion of *G. obamana* above).

Selected specimens examined. BELIZE. **Belize:** Churchyard Pine Ridge, Sibun River, *Gentle 1824* (A, F, K, MICH,

MO, NY); Sibun River, *Gentle 1444* (A, K, MICH, MO, NY, TEX, US). **Cayo:** Chaa Creek, *Arvigo & Cocom 696* (GH, NY, TEX), *716* (NY, TEX). **Corozal:** betw. Sarteneja & Chunox, *Davidse & Brant 32625* (MO, TEX). **Stann Creek:** Middlesex, *Schipp 472* (A, BM, F, G, GH, K, MICH, MO, NY). **Toledo:** near San Antonio, *Gentle 7549* (LL). COSTA RICA. **Alajuela:** Grecia, Los Angeles, camino de Los Angeles a la Laguna de Hule, *González & Perera 998* (MO); San Carlos, Betania de Cutris, *Carvajal V. 406* (MO, TEX). **Cartago:** Turrialba, P. N. Barbilla, Cuenca del Matina, sendero principal Río Dantas, *Mora C. 1790* (MO, NY); Turrialba, Distr. Santa Teresita, *Rivera 1816* (F, K). **Guanacaste:** rd. from Liberia to Hac. Santa María, Rincón de la Vieja Nat. Park, *Garwood et al. 678* (BM, MO); Tilarán, R. B. Monteverde, Cord. de Tilarán, Quebrada Grande, Río Chiquito, Caño Negro, Finca Rodolfo Quesada, *Bello & Cruz 5392* (CAS, MO). **Heredia:** La Selva Biol. Stat., *Folsom 9142* (GH, MO, TEX), Sendero Tres Ríos, *Wilbur & Moore 70292* (MO), OTS field stat., Río Puerto Viejo, *McDowell 1023* (F, MO, US); Sarapiquí, Chilamate, Finca El Bejuco, *Chacón 718* (F, MO, TEX). **Puntarenas:** Osa, Rancho Quemado, Rincón, *Quesada 421* (MO); Puntarenas, Cabo Blanco Nat. Res., S tip of Nicoya Peninsula, *Burger & Liesner 6666* (BM, F, US); Cordillera de Tilarán, Monteverde, cliff edge on Pacific slope, Bajo Tigre trail, *Haber & Zuchowski 10093* (MO, TEX). **San José:** San Francisco, *Donnell Smith 4763* (GH, M, US); Mora, Z. P. El Rodeo, bosque de la Univ. para la Paz, *Cascante 1245* (F, K, MO); Santa Ana, La Lindadora, Pozos, *Jiménez M. 3520* (F, NY). EL SALVADOR. **Ahuachapán:** San Francisco Menéndez, El Corozo, Mariposario, *Rosales 80* (BM, MEXU, MO). **San Salvador:** along rd. San Martín to Laguna de Ilopango, *Standley 22547* (US). GUATEMALA. **Alta Verapaz:** Cubilgüitz, *von Türckheim 7734* (US); Senahu, Finca Secacao, *Véliz Pérez 95.4394* (MO, TEX). **Chiquimula:** E portion of Vera Paz & Chiquimula, banks of Choco River, *Watson 45* (GH). **Escuintla:** near San José, *Standley 64031* (F). **Huehuetenango:** betw. villages of Nentón & Llano Grande, *Castillo Mont & Castillo Mont 1639* (F, GH, MO, NY, US). **Izabal:** vic. of Puerto Barrios, *Standley 24983* (US). **Petén:** Lacandon, *Contreras 3459* (DS, G, LL, US); Tikal, P. N., en camino a Uaxactún, *Tún Ortíz 10* (BM, MICH, US). **Quiché:** Finca Chailá, Zona Reyna, *Skutch 1796* (A, F). **Retalhuleu:** Retalhuleu, *Bernoulli & Cario 2048* (K). **San Marcos:** Finca El Porvenir, along Río Cabús on Potrero Matasán, Volcán Tajumulco, *Steyermark 37575* (A, F). **Santa Rosa:** Cuilapa, *Johnston 1090* (F). **Suchitepéquez:** Finca Mocá, *Skutch 2093* (A, BM, F, NY, US). HONDURAS. **Atlántida:** Lancetilla Valley, near Tela, *Standley 53753* (A). **Colón:** Trujillo, old rd. to Castilla, E of airport to Jericho, *Saunders 873* (BM, F, LL, MO, NY). **Comayagua:** Agua Caliente, vaguada de Ríos Chamo y Humuya, *Nelson et al. 6345* (MEXU, MO, TEX). **Cortés:** orilla del Río Humuya, 40 km N Santa Cruz de Yojoa, *Nelson et al. 5842* (MO, TEX); Santa Cruz de Yojoa, La Ceiba, orilla del Río Yure, *Nelson et al. 7417* (MEXU, MO). **El Paraíso:** Laguna La Presa de San Julián, *Midence 106* (MO). **Francisco Morazán:** above El Zamorano, vic. El Jicarito, *Standley 24872* (A, F). **Gracias a Dios:** rd. to Río Platano, *Wilson 529* (US); Brus Laguna, alrededores del Río Plátano, orilla del río, *Clewell & Cruz 4106* (MO, US); Puerto Lempira, orilla del Río Mocorón, *Nelson & Vargas N. 5071* (MEXU, MO, TEX). **Islas de la Bahía:** Roatán, N slope of mtn., *Barkley & Barkely 39672* (GH). **Olancho:** along Río Olancho, W of main Tegucigalpa–Catacamas Hwy., *Croat & Hannon 64065* (MO, TEX). MEXICO. **Campeche:** Calakmul, Pioneros del Río Xno-ha, *Martínez S. et al. 31773* (MEXU, MO). **Chiapas:** along rd. betw. Teneapa & Yajalón, *Nelson 3287* (GH, US); Zacualpa, *Woronow & Juzepczuk 1249* (F); Ocosingo, a 2 km SE de Nvo. Guerrero, camino Palenque–Boca Lacantum, *Martínez S. 14659* (F, GH, MEXU, MO); Ocosingo, en crucero de Lancanjá–Tzeltal, camino Nvo. Guerrero a Santo Domingo, *Martínez S. et al. 35165* (MEXU, MO; Fig. 2J); Ostuacán, El Chicho, on rd. from Río Copano betw. Pichucalco & Ostuacán, *Burnham 41* (BM, MO). **Hidalgo:** Jacala, Hidalgo–San Luis Potosí border, Km. 343–344 on hwy. below Chapulhuacan, *Moore 5042* (BM, GH, MEXU, MICH). **Oaxaca:** Pochutla, Cerro de Machete, *Reko 6113* (F); Tuxtepec, Chiltepec & vic., *Martinez Calderón 245* (A, LL, US). **Puebla:** Hueytamalco, 1 km hacia el NE de las instalaciones del Campo Exp. Las Margaritas, *Gómez C. & Goméz F. 261* (MEXU, MO). **Querétaro:** Landa de Matamoros, 1.5 km al O de San Onofre, *Rubio 1099* (MEXU). **San Luis Potosí:** Rascón, Río de las Gallinas, *Purpus 5407* (F, GH, MO, NY, US); La Conchita 2 km NE de Xilitla, brecha a Tlamaya, *Tenorio L. & Romero de T. 2481* (MEXU, MO). **Tabasco:** Balancán, Potrero Cercano al poblado el Triunfo, *Menéndez L. et al. 409* (MO); Teapa, 0.34 km al E de Chapingo, Univ. Autón. Chapingo, *Calónico S. et al. 21341* (BM). **Veracruz:** Martínez de la Torre, Coapa, *Ventura A. 20730* (MEXU, MO); Playa Vicente, *Martínez Calderón 2060* (GH, MEXU, MO); San Andrés Tuxtla, 34 km NE del Camino Catemaco–Montepio, *Cedillo T. 3528* (F, MEXU, MO, TEX). NICARAGUA. **Atlántico Norte:** Mt. Liveco, betw. Siuna & Madegrava, *Seymour 5075* (BM, F, GH, MICH, MO, NY, TEX); Bonanza, from mine Plantel ca. 1 km NE, *Stevens 18766* (MO, TEX). **Atlántico Sur:** Est. Exp. El Recreo, zona detrás de la Casa de Piedra y del Ranchón, *Ríos 299* (MO, TEX); vic. of Base Camp, ca. 3.6 km due SE of Cerro San Isidro, Río Kama, *Proctor et al. 27299* (F, NY, TEX, US). **Boaco:** Finca San Jorge, carr. Boaco–Río Blanco, ca. 7 km N de Boaco, *Soza et al. 429* (MO, TEX); 1 km W de San Lorenzo, *Moreno 18590* (MO, TEX). **Chinandega:** Volcán Chonco, *Moreno 25033* (MO). **Chontales:** 24.2 km NE of Villa Sandino along rd. to La Campana, Río Bulún, *Stevens & Montiel J. 30729* (MO); along rd. betw. Santo Tomás & Puente Los Hoyos, toward La Libertad, *Stevens et al. 21505* (MO, TEX). **Estelí:** Condega, Venecia, del alberque Cantagallo 250 m N, *Padilla G. 73* (MO). **Granada:** Isla Zapatera, Finca Garay, Ensenada Sonzapote, costado NE de la isla, *Grijalva P. 2042* (MO, TEX). **Jinotega:** al NE de Wiwilí, camino entre El Carmen y Wamblán, a lo largo del Río Coco, *Araquistain & Castro C. 1835* (MEXU, MO, TEX); along rd. from Hwy. 3 through La Fundadora, betw. La Salvadora & La Palestina, *Stevens & Grijalva P. 15405* (MO, TEX). **Madriz:** Telpaneca, San Jerónimo, *Cárdenas C. 93* (MO). **Managua:** carr. a San Francisco, Hac. San Antonio, *Moreno 5104* (MO, TEX). **Masaya:** Catarina, El Mirador, *Araquistain 412* (MO, TEX). **Matagalpa:** Puente Río La Ponzoña, along rd. W of Río Blanco, *Stevens & Montiel J. 30532* (MO); Río Bijao, near El Carmen, ca. 37 km NE of El Tuma, *Stevens & Moreno 19216* (MO). **Nueva Segovia:** Las Gallineras, orilla de Quebrada La Mula, *Moreno 5876* (MO, TEX). **Río San Juan:** El Castillo, Romerito, de la casa de Antonio Gómez, 600 m E, *Suazo 58* (MO); entrance to Palo Ralo near Acoyapa–San Carlos rd., *Stevens & Montiel J. 27835* (MO). **Rivas:** near Peñas Blancas, 1 km N of border with Costa Rica, *Moore 1829* (MO, TEX); Cárdenas, *Sandino 4096* (MO, TEX). PANAMA. **Bocas del Toro:** Old Bank Island, vic. of Chiriquí

Lagoon, *von Wedel 2045* (MO, NY, US); alrededores de Quebrada Chica, *Correa A. et al. 3816* (F, MO). **Canal Area:** near officer's club, Margarita, *Gentry & Tyson 4830* (MO); betw. Mount Hope & Santa Rita Trail, *Cowell 79* (NY); ca. 1 mi. SW of Cocoli in Rodman Naval Ammun. Depot, *Wilbur et al. 12907* (F, GH, MO, NY, TEX); Barro Colorado Island, laboratory clearing, *Croat 7105* (F, MO, NY). **Chiriquí:** ca. 2 mi. S of Puerto Armuelles, *Wilbur et al. 13578* (F, MICH, MO, TEX); David, *Roy 2* (MO, US). **Coclé:** vic. of El Valle, lower Río Antón, *Allen 103* (F, MO); hills S of El Valle de Antón, *Allen 2863* (F, MO). **Colón:** Chagres, *Fendler 108* (F, MO, US); ca. 1–2 km from Portobelo Hwy. up Río Guanche, *Knapp & Schmalzel 3624* (MO, TEX). **Darién:** Pueblo de Garachiné, carr. entre Garachiné–Sambu, *Duke 9274* (MO, US); trail betw. Cana & Boca de Cupe, vic. of El Real, along trail to Río Pirre, *Stern et al. 625* (MO, US). **Herrera:** Santa María, 5 km W of turnoff from Hwy. 105 to Potuga, *Hammel 5286* (MO). **Panamá:** San José Island, betw. Max Point & South Rd., ca. 55 mi. SSE of Balboa, *Johnston 1173* (BM, GH, MO, US), San José Island, N Loop rd., *Johnston 619* (BM); Panamá, Bella Vista, *Standley 25398* (F, MO, US). **San Blas:** Cangandí, *de Nevers & Herrera 5655* (MO, TEX); trail from dock at airport to Cangandí, *de Nevers et al. 6886* (MO, TEX). **Veraguas:** vic. of Santiago, *Allen 1078* (F, MO, US).

CUBA. **Camagüey:** vic. of La Gloria, *Shafer 60* (NY). **Cienfuegos [Santa Clara]:** Cieneguita, *Combs 93* (F, GH, K, NY, US); Guanaroca Island, betw. Punta Colorado & Rancho Luna, *Hatheway 1015* (B). **La Habana:** Santiago de las Vegas, *van Hermann 21* (BM, F, NY). **Matanzas**: near Matanzas, *Rugel 51* (BM, GH, MO, NY). **Pinar del Río:** betw. Río Cayaguateje & Sierra Guane, *Shafer 10465* (F, MO, NY, US). **Santiago de Cuba:** Morro rd., *Havard 3* (NY). DOMINICAN REPUBLIC. **Hato Mayor:** fuera de la Cueva de Arena, Caseta no. 1 del P. N. Los Haitises, frente a la Bahia de San Lorenzo, *Zanoni et al. 35923* (MO, NY, TEX). **Puerto Plata:** La Cumbre, *Ekman H16101* (LL, US). **San Cristóbal:** 2 km al N de Cambita Garabito, al Tablazo, *García et al. 5657* (F, MO). **Santiago Rodríguez:** Monción, *Valeur 251* (A, F, G, MICH, MO, NY, US). HAITI. **de Nord:** Mt. La Mine, vic. of St. Michel de l'Atalaye, *Leonard 7344* (GH, NY, US). **Nippes:** Massif de la Hotte, gr. Morne Rochelois, Miragoâne, rd. intersection of rte. 386 & 132, *Miller & Sherman 6603* (MO); San Germán, Bo. Rosario Alto, rd. S of 348, Km. 12.6 at Río Nueve Pasos, *Nee 44258* (MO, NY); prope Aguada, ad Río Grande, *Sintenis 5547* (BM, F, G, GH, M, MO, NY); prope Mayagüez in monte Mesa, *Sintenis 36* (BM, G, GH, K, M, NY, PR, US). TRINIDAD & TOBAGO. **Tobago:** Adelphi, *Broadway 3418* (F, G, MO). **Trinidad:** Oropuche Lagoon, *Britton et al. 1147* (GH); La Brea, main rd., *Broadway 9115* (BM, MO). WINDWARD ISLANDS. **Grenada:** Pointe Saline, *Beard 1328* (F). SAINT VINCENT AND THE GRENADINES. **St. Vincent:** rocky ground near sea on Leeward side, *Smith & Smith 1302* (BM, US).

ARGENTINA. **Misiones:** P. N. Iguazú, cataratas de Iguazú, *Vanni et al. 2765* (MICH). BOLIVIA. **Santa Cruz:** Andres Ibanez, llanura, at Jardin Bot. Santa Cruz, on rd. to Cotoca, *Nee 35270* (MO, NY); Ichilo, P. N. Amboró, 1–2 km NE of El Carmen on trail to crossing of Río Surutu, *Nee 41786* (MO, NY). BRAZIL. **Amazonas:** Rio Negro, flum. Solimões, *Spruce 1548* (BM). **Mato Grosso:** picadão que da acesso do Rio Juruena, *Rosa & dos Santos 2120* (MO). **Minas Gerais:** Viçosa, wagon rd. to São Miguel, ca. Km. 2, *Mexía 4625* (A, BM, G, MO); Viçosa, Agric. College lands, *Mexía 4495* (A, BM, MO); Brasília de Minas, *Claussen s.n.* [s.d.] (BM). **Pará:** upper Rio Cupary, plateau betw. Xingu & Tapajos Rivers, *Krukoff 1113* (BM, G). **Roraima:** Vista Boa Res. Ecol. Maracá, betw. Station & Maracá by Rio Urariquera, *Harley 24750* (K, NY). **São Paulo:** Mogi-Guaçu, Martinho Prado, Faz. Campininha, Res. Biol., Mata da Figueira, *Romaniuc N. & Rossi 1165* (F, NY); Luís Antônio, margens do Rio Mogi-Guaçu, *Leitao F. et al. 10101* (BM). COLOMBIA. **Antioquia:** 7 km from Turbo on rd. to Necoclí, *Gentry 9228* (MO). **Bolívar:** Santa Catalina, Loma Las Puas, via Arroyo Grande a Las Canoas, *Cuadros 3285* (MO). **Chocó:** Río Tolo, vic. Guayabal, SE de Acandí, *Quiñones et al. 15* (MO). ECUADOR. **Esmeraldas:** Atacames, betw. Atacames & Súa, *Webster 22835* (MO). **Guayas:** Guayaquil, Bosque Protect. Cerro Blanco, carr. a Salinas, Km. 15, *Rubio et al. 1798* (MO). GUYANA. NW slopes of Kanuku Mtns., in drainange of Moku-moku Creek (Takutu tributary), *Smith 3434* (B, MO). **Essequibo:** Rupununi area, Surama Village, *Acevedo-Rodríguez et al. 3363* (MO). **Rupununi:** Kuyuwini Landing, Kuyuwini River, *Jansen-Jacobs et al. 2376* (B, K). PARAGUAY. **Alto Paraná:** 4 km S de Hernandarias, selva marginal a la Represa Acaray, *Schinini & Caballero M. 27380* (MO); Est. Bertoni (Río Paraná), *Zardini & Florentín 40052* (MO, PY). PERU. **Amazonas:** Condorcanqui, Distr. El Cenepa, Región Nororiental del Marañon, Puerto Mori, Río Comaina, *Vásquez et al. 18917* (MO). **Cajamarca:** San Ignacio, San José de Lourdes, Crucero, *Campos 6156* (MO). **Huánuco:** W of Tingo María, *Schunke V. 5637* (MO, US). **Junín:** Yaupi, *Woytkowski 6510* (MO). **Loreto:** Alto Amazonas, Lagunas, *McDaniel & Rimachi Y. 16518* (MO). **San Martín:** San Martín, W side Río Huallaga, W of Shapaja 2–8 km on trail to Tarapoto, Cerros de Estoraqui, *Belshaw 3198* (MO). **Ucayali:** Coronel Portillo, Yarinacocha, near Pucallpa, *Gentry & Horna 29372* (MO). VENEZUELA. **Barinas:** Riberas del Río Caparo, *Stergios et al. 1781* (MO). **Bolívar:** Piar, Isla en el Lago de Guri, Sect. Danto Manchado, *Aymard et al. 10158* (MO, NY). **Mérida:** Barinas, near Barinitas, *Breteler 4408* (MO, NY). **Miranda:** along Quebrada Chaguarama, 0–4 km SW of Palo Quemado, *Liesner & González 9192* (MO). **Táchira:** arriba de Cementos Táchira hacia Borota, O de San Cristóbal, *Bono 4634* (MO). **Yaracuy:** San Felipe, *Curran s.n.* [28 Dec. 1952] (NY). **Zulia:** headwaters of Río Guasare, Serranía de Perijá, *Gentry 41203* (MO).

12. Gouania pubidisca A. Pool, sp. nov. TYPE: Nicaragua. Chinandega: Chinandega, 12 Jan. 1903, *C. F. Baker 152(673)* (holotype, MO!; isotypes, CAS!, GH!, MICH!, NY!, US [as 673]!). Figures 2K, 13A–D.

Diagnosis. New species similar to *Gouania rosei* Wiggins, but with the disc of the flowers pubescent and the mericarps larger with their inner surfaces drying with the fruit bodies only slightly darker than the wings.

Liana; young branches solid, densely tomentose, or tomentose with additional scattered spreading trichomes, trichomes white, yellow or light red-brown. Leaf blades 4.5–10 × 3–8 cm, ovate or elliptic, membranaceous, adaxial surface drying dark green to dark brown-green, abundantly to sparsely tomentose

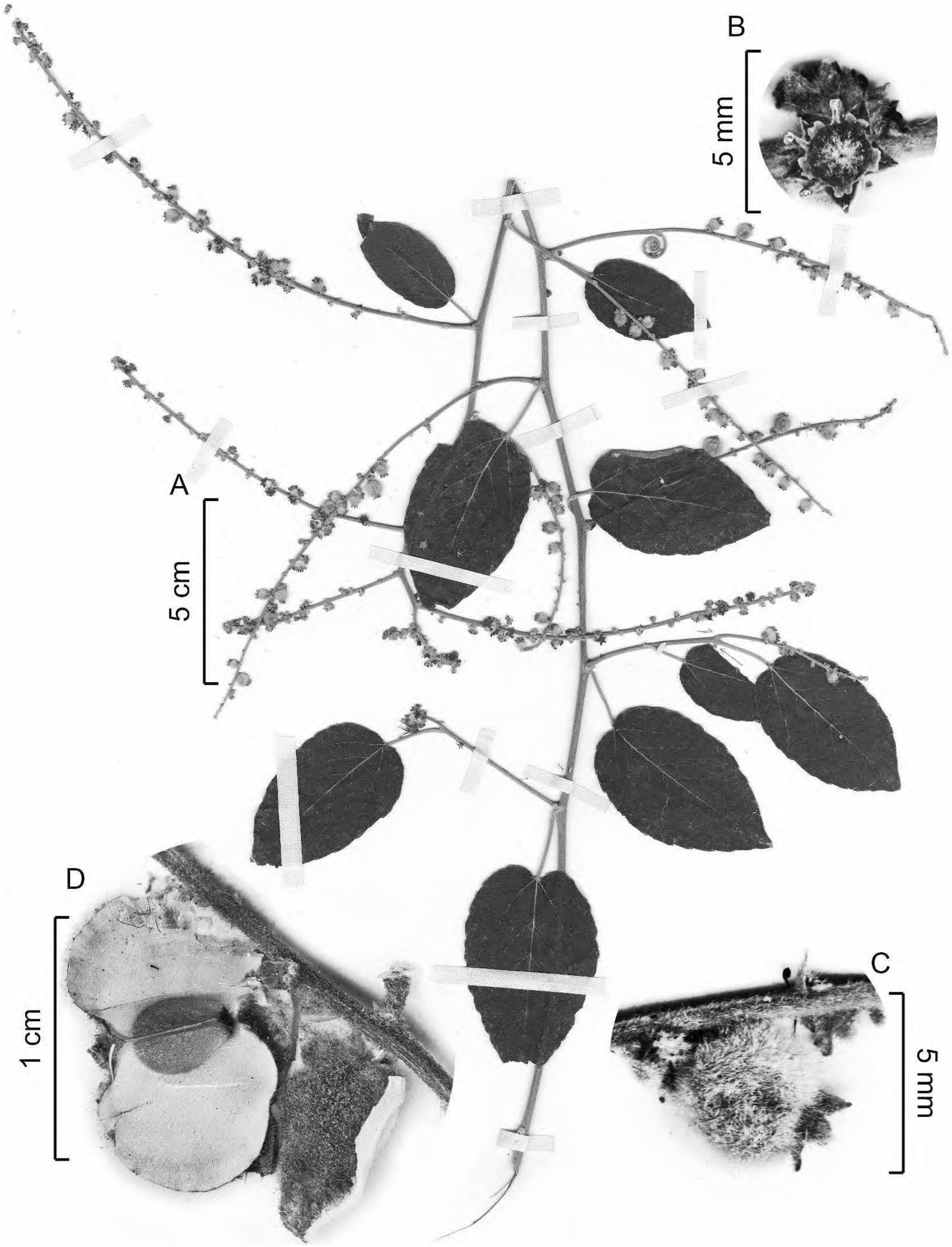


Figure 13. *Gouania pubidisca* A. Pool. —A. Fertile branch with flowers and young developing fruits. —B. Flower at inflorescence node. —C. Young developing fruit. —D. Fruiting node of infructescence with open fruit. A–C scanned from the isotype *C. F. Baker 152 (673)* (NY); D scanned from the paratype *O. Téllez V. 11283* (MO).

with trichomes 0.2–0.5 mm, white, abaxial surface drying light yellow-green often with starkly contrasting black marginal glands, densely pilose to tomentose with trichomes 0.25–0.75 mm, spreading and matted, white or yellow-white, lateral veins 5 or 6(7) per side of midrib, diverging at 45°–60° angles, base cordate, subcordate or rounded, margin crenate or crenulate, 1 to 2 teeth/cm, tooth glands pustular to slightly pulvinate, apex acute-apiculate or obtuse-apiculate (rarely acuminate); stipules unlobed or with small foot, usually caducous, 1.5–4 × 0.5–1.25 mm, erect usually tightly appressed, ovate (rarely lanceolate), acute (rarely acuminate), foot (if present) 0.2–0.75(1.5) × 0.1–0.25 mm, curving downward, ovate (rarely subulate), acute; petioles 5–20 mm. Inflorescence with longest racemiform part 15–28 cm, indumentum of rachis similar to that of young branches, bract of cyme 1.25–3 mm, lanceolate or ovate, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.5 mm, hypanthium and sepals externally densely pilose with trichomes yellow or yellow-white; sepals 0.75–1.1 mm; petals 0.6–0.9 mm; stamens with filaments 0.35–0.6(0.7) mm, anthers 0.15–0.25(0.3) mm; disc excluding lobes 0.9–1.6 mm diam., entire disc, excluding lobes, pubescent to trichomes distributed only along annulus and in lines, long to short, radiating from annulus, disc lobes ca. 0.15–0.3 × 0.3–0.7 mm at apex, transversely rectangular, generally apically bilobed, 1/5–1/3 length of sepals; style glabrous or pubescent. Young fruits densely velutinous, trichomes yellow or yellow-white; mature mericarps butterfly-shaped (Fig. 2K), the wings attached to apex and base of fruit body as well as sides, externally drying green-brown to light yellow-brown, darker over fruit body, abundantly pilose to velutinous with trichomes 0.25–0.5 mm, white to light red-brown, internally drying yellow-white or yellow-green on wings, contrasting only slightly with somewhat darker or red-tinted fruit body, sometimes pale red along margin of fruit body or an additional concentric pale red ring on wings, fruit body 4–7 mm high, wings 7–10 mm high, distance between highest points of 2 wings 4–7 mm, width of mericarp 10–14 mm, 2–2.5× height of fruit body, width of fruit body 3–3.2 (3.75) mm, 1/5–1/3 width of mericarp; seeds 2.5–3.25 × 1.6–2.75 mm, shiny brown.

Habitat and distribution. *Gouania pubidisca* is known from Pacific Mexico (Nayarit, Guerrero, Oaxaca, and Chiapas), central Guatemala (Dept. Guatemala), El Salvador, and Pacific Nicaragua (Chinandega, Managua, and Granada). It has been found in deciduous forests, at 40–1000 m elevation (Fig. 4A).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania pubidisca* is known from only 29 collections scattered in dry deciduous forests from Nayarit, Mexico, to Granada, Nicaragua, between 40 and 1000 m elevation. The species has an estimated area of occupancy of 96 km² and, as 71% of its collections fall outside of protected areas, further study is strongly recommended to determine its conservation status.

Phenology. *Gouania pubidisca* has been collected in flower from August to February.

Discussion. *Gouania pubidisca* is most similar to *G. rosei* of Pacific Mexico (Baja California Sur, Sonora, and Chihuahua south to the Tehuantepec District of Oaxaca), with which it can be confused when sterile or in flower. *Gouania rosei* differs in having the floral disc totally glabrous or with trichomes restricted to the annulus, the ratio of disc lobes to sepals 1/3–2/5(–1/2), and smaller mericarps (height of wings 4–6 mm and width of mericarp 6–9 mm), with the inner surface strongly bicolored. In addition, the leaves of *G. pubidisca* tend to dry bicolored, with the adaxial surface drying much darker than the abaxial surface, while in *G. rosei* both surfaces dry yellow-green. Most specimens of *G. pubidisca* have been misidentified as *G. polygama* (Oaxaca, Mexico, to South America and West Indies), which differs in having the trichomes of the floral disc restricted to the annulus, the disc lobe to sepal ratio (1/3–)2/5–3/5(–2/3), disc lobes often apically tapering and the mericarps dumbbell-shaped and glabrous. Fruiting specimens of *G. pubidisca* can be confused with *G. velutina*. However, even in fruit *G. velutina* usually retains some of its stipules (lower lobe orbicular to reniform and 4–11 mm wide) and some of the sepals and disc lobes (disc lobes lanceolate and acuminate and 1/2–1× length of sepals). The mericarps of *G. velutina* are also nearly truncate apically, and the internal surfaces have red lines radiating from the fruit body. Following the work of Reissek (1861) and Suessenguth (1953a), *G. pubidisca* would belong to their section I, characterized by the pubescent floral disc. The only other species from Central America in this section would be *G. hypoglauca*, which is easily distinguished from *G. pubidisca* by the unusual indumentum of its abaxial leaf surface.

The paratype *Soeharto et al. 7237* (in fruit) differs from all the other known fruiting collections of *Gouania pubidisca* in having only a few trichomes retained on the floral disc.

Paratypes. EL SALVADOR. **Ahuachapán:** San Benito, Peña los Escobos, *F. Chinchilla P. s.n. (ISB-00696)* (B, F, MO); San Francisco Menéndez, El Corozo, Mariposario, *J. M. Rosales 1645* (B, BM, MO), *J. M. Rosales 2441* (MO); Finca Santa Lina, ca. 6 km al S de Ahuachapán, *J. L. Linares & C. A. Martínez 2013* (MEXU). **La Unión:** San Carlos, Golfo de Fonseca, *G. W. Barclay 2665* (BM, K). **Santa Ana:** a la orilla de la carr. a Metapán, entre la Hda. El Milagro y la Hda. San Cayetano, *J. L. Linares & C. A. Martínez 849* (MEXU); Metapán, P. N. San Diego-La Barra, *D. Rodríguez & A. Tejada 2133* (MO). GUATEMALA. **Guatemala:** Palencia, on rd. Guatemala City–El Progreso, Km. 30, *D. D. Soejarto et al. 7237* (F). MEXICO. **Chiapas:** carr. Acapethua–Acacoyagua, Soconusco, *A. Aquino 207AA* (MEXU); Arriaga, *C. D. Mell 2184* (NY, US); Cintalapa, 5 km W of Rizo de Oro, *D. E. Breedlove 36724* (MO); Escuintla, Mt. Ovando, *E. Matuda 17046* (F, MEXU); Motozintla, 25–27 km NE of Huixtla along rd. to Motozintla SW of Tolimán, *D. E. Breedlove 28594* (LL, MO); Tonalá, en las cercanias de la zona arqueologica Iglesia Vieja, *L. O. Alvarado-Cárdenas & A. Reyes-García 745* (MEXU, MO); Paderon [Paredón], Tonalá, *E. Matuda 16966* (F, MEXU). **Guerrero:** Atoyac–San Juan, *G. B. Hinton & J. C. Hinton 10926* (GH, K, US). **Nayarit:** Compostela, camino de terracería de Valle de Banderas a El Coatante, *O. Téllez V. 11283* (MEXU, MO). **Oaxaca:** Juquila, 2–10 km N of Puerto Escondido, *R. McVaugh 22445* (MICH); Distr. Tamiltepec [Jamiltepec], Huazolotitlán a Collantes, *C. Conzatti 4402* (MEXU), *4407* (MEXU, NY); Juchitán, Mpio. de Asunción Ixtaltepec, *E. E. Lebrija T. & E. A. Pérez G. 42* (MO); Tehuántepec, El Manguito, al sur de El Limón, *R. Torres C. 4170* (MEXU, MO). NICARAGUA. **Chinandega:** Mpio. Chinandega, falda de Volcán Casita, entrada Los Laureles, Hacienda Versalle, *I. Coronado G. & J. Reyes 6462* (MO). **Granada:** Granada, *P. Lévy 378* (G); Volcán Mombacho, 1 km al este de La Luz, *P. P. Moreno & J. C. Sandino 6488* (MEXU, MO, TEX), W slope of Volcán Mombacho, along rd. to Finca La Luz, 2 km E of (above) last fork, *W. D. Stevens & O. M. Montiel J. 33195* (MO; Fig. 2K). **Managua:** Cuatro Esquinas de Ticuantepe, camino entre Santo Domingo y Las Nubes, *P. P. Moreno 4383* (MO, NY, TEX).

13. Gouania rosei Wiggins, Contr. Dudley Herb. 4: 20. 1950. Replaced name: *G. mexicana* Rose, Contr. U.S. Natl. Herb. 3: 314. 1895, non *Gouania mexicana* Sessé & Moc., Fl. Mexic., ed. 2: 236. 1894. TYPE: Mexico. [Sinaloa]: Culiacán, 27 Aug.–25 Sep. 1891 [27 Aug. to 15 Sep. 1891, GH, MICH, US labels], *E. Palmer 1491* (lectotype, designated here, US-235108!, digital image 00094523!; isolectotypes, GH!, MICH!, US-235109!, digital image 00094522!, US-1491573, digital image 00901591!). Figure 2L.

Liana; young branches solid, abundantly to densely tomentose or pilose or tomentose with several longer, spreading trichomes, trichomes white, yellow-white or white with scattered light red-brown trichomes. Leaf blades 4.2–13 × 2–8 cm, elliptic, oblong, or ovate, membranaceous, both surfaces drying yellow-green, densely to abundantly pilose (sometimes with age trichomes sparse above and scattered below) with trichomes 0.1–0.5 mm, kinky, white, lateral veins (4)5 to 7 on either side of midrib, diverging at 45°–70° angles, base cordate, subcordate, or rounded, margin crenate or crenulate to nearly entire, 1 to 2 teeth/cm, tooth glands pulvinate to cupular, apex acute to acuminate (rarely obtuse to rounded); stipules unlobed (rarely with subulate foot), generally caducous, 1.75–5 × 0.5–1 mm, erect, lanceolate, acuminate, the tip sometimes long extended and flexuous, foot (if present) 0.5–1 × 0.05–0.1 mm, curving downward, subulate; petioles 5–20 mm. Inflorescence with longest racemiform part 5.5–16(20) cm, indumentum of rachis similar to that of young branches, bract of cyme 1–4.5 mm, lanceolate or narrowly triangular, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.5(0.75) mm, hypanthium and sepals externally abundantly to densely sericeous with trichomes white or yellow-white; sepals 0.6–1.3 mm; petals 0.6–1.1 mm; stamens with filaments 0.5–0.75 mm, anthers 0.15–0.3 mm; disc excluding lobes 1–2 mm diam., annulus glabrous or with few to numerous trichomes, disc otherwise glabrous, disc lobes 0.2–0.4(–0.5) × (0.15–)0.25–0.5(0.7) mm at apex, transversely rectangular, square, or slightly narrowed apically (rarely lanceolate and acuminate), generally apically bilobed, 1/3–2/5(–1/2) length of sepals; style usually pubescent. Young fruits densely to abundantly velutinous to pilose, trichomes yellow-white; mature mericarps butterfly-shaped (Fig. 2L), the wings attached to apex and base of fruit body as well as sides, externally drying yellow-brown or yellow-green, darker over fruit body, densely to abundantly sericeous to pilose (or sometimes trichomes scattered on wings) with trichomes 0.2–0.75 mm, white, internally drying yellow-white on wings, contrasting markedly with dark red-brown fruit body, fruit body 4–5 mm high, wings 4–6 mm high, distance between highest points of 2 wings 3–5(6) mm, width of mericarp 6–9 mm, 1.25–2× height of fruit body, width of fruit body (2.5–)3–4 mm, (1/3)1/2 width of mericarp; seeds 2.5–3.5 × 1.9–2.6 mm, shiny brown.

Habitat and distribution. *Gouania rosei* is known from Pacific Mexico, near the tip of Baja California Sur, and from Sonora and Chihuahua south to the Tehuántepec District of Oaxaca. The species is found in subdeciduous, deciduous, and thorn forests, at 0–750(–1330) m elevation (Fig. 5A).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania rosei* is known from 130 specimens from Pacific Mexico and has an estimated area of occupancy of

almost 400 km². Because the species is restricted to dry to very dry habitats and 70% of its area of occupancy is in unprotected areas, further study is recommended to establish its conservation status.

Phenology. *Gouania rosei* has been collected in flower from August to October.

Discussion. *Gouania mexicana* was published by Rose (1895), based on the two syntypes: *Palmer 1491* and *Palmer 1694*. The specimen *Palmer 1491* (US-235108) has the most diagnostic features of the species, with the mericarps small, pubescent and internally drying bicolored, and the small, unlobed stipule. The US sheet (US-235108) is hand-annotated by Rose on the lowermost left-hand label, and therefore *Palmer 1491* is here selected as the lectotype for *G. mexicana* and its replacement name, *G. rosei*.

Gouania rosei is very easily recognized in fruit, but *G. pubidisca*, *G. lupuloides*, *G. conzattii*, and *G. polygama* all have geographic distributions that overlap with *G. rosei* and may be confused with *G. rosei* when fruits are absent. See the discussions under *G. pubidisca* and *G. conzattii*. Both *G. lupuloides* and *G. polygama* differ from *G. rosei* in their bilobed stipules and nearly glabrous mericarps with the inner surface only slightly darker over the fruit body; additionally the mericarps of *G. lupuloides* are usually larger than those of *G. rosei*, with the width of the mericarp (8)9–16 mm and height of wings (5)6.6–12 mm; those of *G. polygama* are dumbbell-shaped versus butterfly-shaped in *G. rosei*. *Gouania lupuloides* never has trichomes on the floral disc annulus and usually has longer pedicels in flower ([0.5–]1–3[–4] mm) than *G. rosei*. *Gouania polygama* overlaps geographically with *G. rosei* only in Oaxaca and has a larger disc lobe to sepal ratio, (1/3–)2/5–3/5(–2/3), with the disc lobes often apically tapering.

Selected specimens examined. MEXICO. **Baja California Sur:** La Hiedra, near headwaters of arroyo NW of El Encinal, *Carter & Chisaki 3468* (B, BM, MEXU, MICH, MO, NY, TEX, US), *3590* (BM, MEXU, MICH); 1 mi. N of Rancho El Aguaje, SSE of Pescadero, *Moran 19034* (GH, LL, MICH, MO; Fig. 2L, US); La Paz, S side of Arroyo de León, *Wiggins et al. 500* (US); 6–10 mi. SE of Todos Santos–Cabo San Lucas Hwy. on small rd. to Rancho La Burrera, *Breedlove & Axelrod 43216* (MEXU). **Chihuahua:** Río Aros, in canyon, *LeSueur 1252* (F, TEX); Guasaremos, Río Mayo, *Gentry 2378* (F, K, MEXU, MO). **Colima:** along Hwy. 80, 6.6 mi. by rd. SE of El Colomo, *Breckon et al. 1094* (F, GH, TEX); Manzanillo, *Ferris 6052* (A, US); Tecomán, La Salada, 21 km SE de Colima, carr. Colima–Manzanillo, *Santana M. 918* (MEXU). **Guerrero:** Acapulco & vic., *Palmer 103* (A, F, GH, MICH, MO, NY); Atoyac de Alvarez, a 4 km al NE de Atoyac camino a Paraíso, *Soto N. 11696* (MEXU, US); Coyuca de Benítez, *Meza A. 113* (MEXU); Petatlán, 9 km al NO de la desv. a El Camalote, *Soto N. et al. 5972* (MEXU, TEX). **Jalisco:** La Huerta, Rancho El Paraíso, *Lott & Solís M. 641* (MEXU, TEX); La Huerta, Cumbres section of Rancho Cuixmala, *Lott et al. 2899* (MEXU, MICH, NY); La Huerta, Rancho la Mesa y Carrizalillo, *Flores et al. 3024* (MICH, TEX); La Huerta, Chamela, camino entrada, *Ayala 204* (F, MEXU, MO, TEX); La Huerta, Rancho Cuixmala, *Ayala 1121* (MICH, MO). **Michoacán:** Cerro Zinaparo, 3.5 km SE de Churintzio, *Trejo 2524* (MEXU). **Nayarit:** P. H. Aguamilpa, *Flores F. et al. 2941* (MEXU, MICH, MO); Nayar, 8 km NW de San Juan Peyotán, *Flores F. & Tenorio L. 1203* (MEXU, MICH, MO); Nayar, 3 km S de San Juan Peyotán, *Flores F. & Ramírez R. 2675* (MEXU, MICH, MO); Santa María del Oro, 19 km E de San José de Mojarras, *Ramírez R. & Flores F. 698* (MEXU, MICH, MO). **Oaxaca:** Pochutla, Mpio. Santa María Huatulco, *Sánchez M. & Nava Zafra 513* (MEXU); Pochutla, Mpio. Santa María Huatulco, *Nava Zafra et al. 1313* (MEXU); Tehuántepec, Mpio. de Santiago Astata, Tapanalá, *Castrejón R. et al. 976* (MEXU, MO); Tehuántepec, Mpio. de Santiago Astata, Barra de la Cruz, Laguna del Potrerón, *Elorsa C. 2398* (MEXU, MO); Tehuántepec, Mpio. Santiago Astata, Barra de la Cruz, *Elorsa C. 991* (MEXU, TEX). **Sinaloa:** [Imala] "Ymala," *E. Palmer 1694* (syntype, US; isosyntype, GH); Cerros de Navachiste ca. Bahia Topolobampo, *Gentry 14326* (MEXU, TEX, US); ca. 2.6 mi. from Hwy. 15 along rd. to microwave tower, ca. 17 mi. SE of Emcosa, *Stevens & Fairhurst 2047* (GH, MO, TEX); a 56 km de Badiraguato rumbo a Surutato, *Vega A. et al. 2466* (MEXU); Culiacán, Tacuichamona, *Valverde R. 160* (MEXU); Culiacán, poblado de Jesus María y cercanias de la Presa Adolfo López Mateos (El Varejonal), *Vega A. et al. 3294* (MEXU); Rosario, Cacalotan, El Habal, *González Ortega 924* (MEXU). **Sonora:** Sierra Bojihuacame, SE of Cd. Obregón, *Gentry 14493* (LL, US); Alamos, *Palmer 676* (F, GH, MEXU, NY); Bacadéhuachi, *Hartman 258* (GH); Navojoa, Ejido Francisco Solis, 7 km (by air) ENE of Est. Luis, *van Devender et al. 98–2115* (MEXU, NY); small arroyo 10 mi. NW of Ures, *Wiggins 7350* (MICH).

14. Gouania stipularis DC., Prodr. 2: 39. 1825. *Phylica scandens* Sessé & Moc., Pl. Nov. Hisp. 39. 1887 [1888]. TYPE: Mexico. Michoacán: [Apatzingán] "Apatzingam" (from Sessé & Mociño, 1887 [1888]), *Torner Collection no. 0989* [= *Hunt Institute 6331.0989*: the plate numbered by Sessé & Mocino as *441* of "Ic. Fl. Mex."] (holotype, *Torner Collection no. 0989* not seen, digital image! [lectotype for *P. scandens* designated by McVaugh [2000: 452], *Torner Collection no. 0989*]). EPITYPE: Mexico. Jalisco: Mpio. La Huerta, 0.9 km de la carr. Puerto Vallarta–Barra de Navidad, ca. 7 km al SE de la Est. Biol. Chamela, sobre el camino a "El 25" (IMSS Comun.), Careyes, 27 Oct. 1981, *E. J. Lott & J. A. Solís M. 622* (epitype, designated here, MEXU!; isoepitypes, MICH!, MO!, TEX!). Figures 1H, 2M.

Gouania pallida Rose, Contr. U.S. Natl. Herb. 5: 138. 1897. TYPE: Mexico. Guerrero: Acapulco, Dec. 1895 [Oct. 1894–Mar. 1895, A, BM, F, GH, K, MO, NY, US

labels], *E. Palmer 228* (holotype, US!; isotypes, A [as *238*, corrected to *228*]!, BM [as *238*]!, F!, GH!, K [as *238*, corrected to *228*]!, MO [as *238*, corrected to *228*]!, NY [as *238*]!, US [as *238*, corrected to *228*]!).

Liana; young branches solid, glabrous. Leaf blades 7–15 × 3.1–8.5 cm, elliptic, membranaceous, both surfaces green, glabrous or with few trichomes on venation 0.25–0.5 mm, appressed, white to red-brown, lateral veins (5)6(7) per side of the midrib, diverging at 30°–45° angles, base cordate to subcordate (rarely inaequilaterally truncate), margin crenate or crenulate (rarely serrate), 1 or 2 teeth/cm, tooth glands cupular (rarely pulvinate), apex acuminate; stipules 3-lobed (Fig. 1H), at least some retained into mature fruit, upper lobe 8–15 × 10–30 mm, curving downward (rarely ascending), foliaceous, reniform, rounded, middle lobe 3–8 × 0.75–3 mm, curving upward (at least at tip), lanceolate, acuminate, lower lobe 5–12 × 6–12 mm, curving downward, foliaceous, orbicular to wide spatulate, rounded; petioles 10–30 mm. Inflorescence with longest racemiform part 15–29 cm, rachis sericeous to pilose with trichomes white, yellow, or ferruginous, bract of cyme 2.25–4.5 mm, variously 3-lobed and similar to stipules or unlobed and oblong-rounded to ovate, acute or lanceolate, acuminate, cymes usually appearing sessile but peduncle on occasion developing to 10 mm, mature flowers with pedicels 2–3.5 mm, hypanthium and sepals externally sparsely to densely sericeous with trichomes white to yellow-brown, sometimes mixed with ferruginous; sepals (0.75)0.9–1.3 mm; petals 0.75–1.2 mm; stamens with filaments 0.6–1 mm, anthers 0.25–0.35 mm; disc excluding lobes 1.2–1.7 mm diam., glabrous, disc lobes 0.1–0.35 × 0.5–0.9 mm at apex, transversely rectangular, generally apically bilobed, 1/10–1/4 length of sepals; style glabrous. Young fruits with few appressed to spreading trichomes, white or white and ferruginous; mature mericarps butterfly-shaped (Fig. 2M), the wings attached to apex and base of fruit body as well as sides, externally drying yellow-brown, darker over fruit body, glabrous or with few scattered trichomes near apex of fruit body, ca. 0.2 mm, white, internally drying yellow-white on wings usually contrasting markedly with medium to dark brown (rarely light brown) fruit body, fruit body 4–6 mm high, wings 5–7 mm high, distance between highest points of 2 wings 4–6 mm, width of mericarp 6–11 mm, 1–2× height of fruit body, width of fruit body 3–4.5 mm, 1/3–1/2 width of mericarp; seeds 3.1–3.5 × 2–2.75 mm, shiny brown.

Phenology. *Gouania stipularis* has been collected in flower from October to June, with a primary anthesal peak in October and November and a secondary peak in March.

Habitat and distribution. *Gouania stipularis* is known from Pacific Mexico from Nayarit to the northern border of Oaxaca. It is found in subdeciduous or deciduous forests or thickets, at 0–1100 m elevation (Fig. 4B).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, *Gouania stipularis* is known from 36 collections from the dry forests of Pacific Mexico. It has an estimated area of occupancy of 116 km² and, with 65% falling in unprotected areas, further study is recommended to establish its conservation status.

Discussion. De Candolle published *Gouania stipularis* citing "fl. mex. ic. ined." (de Candolle, 1825: 39). Alphonse de Candolle (1874: index, page 3) indicated as the type of *G. stipularis* the plate of "Icones florae mexicanae ineditae" (de Candolle, 1874: introduction) that was the source of the tracing number *178* (Calques des Dessins). Tracing number *178* is a copy of the original plate *441* of Sessé and Mociño (de Candolle, 1825: 39) "Fl. mex. ic. ined." The original plate *441* (plate number *0989* of the Torner Collection) is annotated in Augustin de Candolle's handwriting as "*Gouania ? stipularis*" and was apparently the only material de Candolle had available to him of this species, and is therefore the holotype (cf. Art. 9.1, McNeill et al., 2012). Sessé and Mociño, 1887 (1888: 39), also cited plate *441* for *Phylica scandens*, and McVaugh (2000), finding no specimens in the Sessé and Mociño herbarium with this name, selected this plate as the lectotype of *P. scandens*.

Unfortunately, the Torner plate is more artistic than informative, particularly with respect to the stipules. Some of the stipules in the plate are fused and amplexicaule, while others are separate and widely ovate. None are reniform as described by Sessé and Mociño. The stipules of *Gouania stipularis* are 3-lobed, with two lateral large lobes, one reniform and one more or less orbicular to broadly spatulate, and a small lanceolate central lobe. To assist in the application of the names *G. stipularis* and *Phylica scandens*, a flowering specimen at MEXU, *Lott & Solís M. 622*, is chosen as the epitype, with duplicates at MICH, MO, and TEX.

The name *Phylica scandens* was replaced in Sessé and Mociño (1894) by *Gouania domingensis* and *G. mexicana* (for the latter, see the discussion below *G. polygama*). The diagnosis of *G. domingensis* used here by Sessé and Mociño (1894: 69) is identical to

that used previously for *P. scandens* (excluding citation of the icones number), and while the description differs in wording, it referred to essentially the same taxon. I believe (as did McVaugh, 2000) that Sessé and Mociño were here misapplying *G. domingensis* L. (see discussion under *G. lupuloides*) and not publishing a new species (as interpreted by Nelson, 1997).

Rose (1897) published *Gouania pallida*, separating it from *G. stipularis* based on differences in stipule shape, leaf base and margin, and raceme length. The type of *G. pallida* fits within the taxonomic concept of *G. stipularis* here employed, and is therefore placed in synonymy under that name. The type was cited by Rose as *E. Palmer 228*, Acapulco, December 1895, and the holotype at US is labeled accordingly (but with the date as October 1894 to March 1895). However, the isotype at US was originally numbered as *238*, with a *2* written over the *3*. A number of the duplicates were distributed with the *238* number corrected to *228* or, in the case of the MO sheet, with a note saying it should be corrected. The BM and NY sheets are assumed also to be correctable to *228*.

Gouania stipularis is easily recognized by its 3-lobed stipules, with the lateral lobes large and foliaceous. However, specimens of *G. lupuloides*, which has bilobed stipules, can on occasion have the lower lobe large and foliaceous (Fig. 1F), and these specimens are sometimes misidentified as *G. stipularis*. Hemsley (1879) cited *Linden 893* (K not seen), from the Yucatan Peninsula, as *G. stipularis*, and Standley (1930) included *G. stipularis* as from the Yucatan Peninsula, based on a *Linden* specimen (without collection number), but suggested that the locality of that collection was doubtful. I have not seen *Linden 893*, believed to be at K, but not included in their loan to me, nor have I seen *G. lupuloides* with foliaceous stipules from the Yucatan Peninsula. However, J. J. Linden visited Veracruz on the same expedition that took him to the Yucatan Peninsula, sailing from the port at Veracruz to Campeche (Ceulemans, 2006), and specimens of *G. lupuloides* with the lower lobe of the stipules large and foliaceous are known from Veracruz, so *Linden 893* is perhaps a mislabeled specimen of *G. lupuloides* from Veracruz. Suessenguth (1953a) also cited *G. stipularis* from the Yucatan Peninsula, presumably from Standley (1930). Fernández (1986) treated *G. stipularis* from Veracruz based on *Calzada 1684* (MEX, XAL) and *Perino 3218* (CHAPA, ENCB, MEXU, NY). I have examined duplicates of *Calzada 1684* (BM, F, MEXU, Fig. 1F) and *Perino 3218* (MEXU, NY), and both are *G. lupuloides*.

A few specimens of *Gouania stipularis* (such as *Martínez S. et al. 4406*) have lost all their stipules, and these are difficult to separate from *G. lupuloides* because they overlap in most other characteristics. However, *G. stipularis* can usually be separated from *G. lupuloides* by the combination of glabrous young branches (vs. pubescent), nearly glabrous leaves (vs. variable in *G. lupuloides*) with usually six or seven lateral veins per side of midrib (vs. [three]four or five, less frequently six veins), the relatively small disc lobes, 1/10–1/4 length of sepals (vs. 1/5–2/5[1/2] length of sepals), mericarps with wings 5–7 mm high and fruit bodies usually strongly contrasting in color with wings (vs. wings [5]6.6–12 mm and fruit bodies only slightly to moderately contrasting with wings).

Additional specimens examined. MEXICO. **Colima:** 11 km W de Itlahuacán, camino a Agua de la Virgen, *Martínez S. et al. 4406* (MEXU, TEX). **Guerrero:** Montes de Oca, San Antonio, *Hinton & Hinton 14087* (GH, K, LL, NY, US); Distr. Adama, Temisco, lower barranca de la Guacamaya, *Mexía 8887* (B, F, GH, MO; Fig. 2M, NY, US); Acapulco, P. N. El Veladero, *Noriega A. 477* (MEXU); Chilpancingo, Rincón de La Via, *Kruse 114* (MEXU); Coahuayutla, Los Alacranes, *Calónico S. 18283* (MEXU); José Azueta, Cerro Bolonche, E del mirador del Parque Ecol. La Vainilla, *Gallardo H. et al. 213* (MEXU); Mochitlán, Rincón de La Via, *Kruse 19631128-134* (MEXU); Mochitlán, Rincón de La Via, *Kruse 5570* (B, M, MEXU, MO), *19630323-135* (M); San Luis Acatlán, Atotonilco, *Martínez S. et al. 3564* (MEXU). **Jalisco:** camino El Central en el cruce con el sendero El Tejó, dentro de la Est. Biol. Chamela, UNAM, *Dominguez-Mariani 1233* (MEXU); Arroyo Colorado, ca. 3 km O del camino Eje Central, dentro de la est. Biol. Chamela, *Dominguez-Mariani & Calónico S. 896* (MEXU); 2.5–4 mi. (N of) La Cuesta, rd. to Talpa de Allende, *McVaugh 21214* (MICH); Acatic. Quimixto, *Mexía 1186* (BM, MICH, MO, NY, US); Autlán, 5 mi. N of Bahía de Navidad, *McVaugh 20903* (MICH); Cabo Corrientes, valley of Río las Juntas, *McVaugh 25434* (MICH); La Huerta, Est. Biol. Chamela, *Pérez J. et al. 313* (MEXU), *Lott & Bullock 1436* (MEXU, MO, TEX); La Huerta, brecha y playas La Manzanilla–El Tamarindo, *Villarreal 7141* (MICH); La Huerta, Rancho Cuixmala, *Ayala 1232* (MEXU, MICH, MO); La Huerta, UNAM, 8 km E de Chamela, *McVaugh 25146* (MICH); Tolimán, camino de San Pedro Toxín a Toxín, *Ramírez D. 2939* (MEXU); Tuxcacuesco, E-central Sierra de Manantlán in pass betw. Cerro Grande y Cerro en Medio, *Cochrane et al. 12294* (MICH). **México:** Temascaltepec, Limones, *Hinton 6723* (BM, F, GH, K). **Michoacán:** W facing slopes of Sierra Madre del Sur, 32 km N of Playa Azul, *King & Soderstrom 4943* (MEXU, MICH, NY, TEX, US). **Nayarit:** Islas Marías, Isla María Magdalena, *Chiang C. & Flores F. 1069* (MEXU, MO); Compostela, a 10 km al W de Mazatán por el camino viejo a Las Varas, *Téllez V. & Chiang C. 9718* (MEXU, MO; Fig. 1H); Tepic, en el Km. 3–5 del camino al Ingenio La Escondida, *Téllez V. & Salinas T. 11919* (MEXU, MICH, MO); Tepic, on bajada ca. 19 mi. NW of Tepic, hwy. to Mazatlán, *McVaugh & Koelz 724* (MICH). **Oaxaca:** Putla, Puente de la Pastora, 2 km S of Cacahuatepec, *McVaugh 22221* (MICH).

15. Gouania velutina Reissek in Mart., Fl. Bras. 11(1): 105. 1861. TYPE: [Guyana]. "Guyana interiore," *R. H. Schomburgk 747* (holotype, W not seen, W holo. fragm. at F!, W photo F neg. 32603!; isotypes, BM-544412!, BM-796336!, GH!, K!). Figures 1I, 2N.

Gouania colurnifolia Reissek in Mart., Fl. Bras. 11(1): 107. 1861, as "*colurnaefolia*." TYPE: Brazil. Ceará: "Villa do Crato," Oct. 1838, *G. Gardner 1523* (holotype, W not seen; isotypes, BM-54408!, BM-544409!, F!, G not seen, G fragm. at F!, G photo F neg. 23292!, GH!, K!, NY-232902!, NY-232903!). [Locality taken from BM-54408, BM-544409, NY-232903.]

Liana; young branches solid or hollow in part, densely villous or velutinous, trichomes light red-brown or white-yellow. Leaf blades 4–10.5 × 3–8 cm, elliptic or widely elliptic, membranaceous to subcoriaceous, adaxial surface drying dark green-brown or dark green-black, densely to abundantly pubescent, glabrescent with age, with trichomes 0.2–1 mm, straight to slightly curved, ± appressed, ascending or spreading in all directions, white to light red-brown, abaxial surface drying pale green or pale yellow-green, densely pilose to tomentose with trichomes 0.2–1 mm, spreading and matted, white and light red-brown, lateral veins 5 to 7 per side of the midrib, diverging at 45°–60° angles, base cordate or subcordate, margin crenate or crenulate (rarely serrulate), 1 to 3 teeth/cm, tooth glands cupular or less frequently pulvinate, apex obtuse-apiculate or rounded-apiculate to short-acuminate, less frequently acute to acuminate; stipules 2-lobed (Fig. 1I), at least some retained into young fruit, upper lobe 4.25–11 × 1–4 mm, curving upward, lanceolate, acuminate, often with long extended and flexuous tip, lower lobe 3.5–10 × 4–11 mm, curving downward, margins recurved to stipule folded in half to cucullate, foliaceous, orbicular to reniform, often with extended tip or 2 long teeth; petioles 4–10(15) mm. Inflorescence with longest racemiform part 7–17 cm, rachis velutinous to villous with trichomes light red-brown or white-yellow, bract of cyme 2.5–3.5 mm, lanceolate, acuminate, cymes appearing sessile, mature flowers appearing sessile to pedicels to 0.75 mm, hypanthium densely velutinous with trichomes light red-brown or white-yellow; sepals 0.6–1 mm, externally densely villous, pilose or sericeous, trichomes light red-brown or white-yellow; petals 0.6–0.8 mm; stamens with filaments 0.4–0.75 mm, anthers 0.2–0.3 mm; disc excluding lobes 1–1.6 mm diam., glabrous or less frequently with few trichomes along annulus, disc lobes 0.4–0.6 mm, lanceolate, acuminate, not lobed, (1/2–)2/3–1× length of sepals; style pubescent at base. Young fruits densely velutinous, trichomes light red-brown or light yellow; mature mericarps butterfly-shaped (Fig. 2N) but with emargination at base only, the apex truncate or nearly truncate (less frequently rounded to obtuse), the wings attached to apex and base of fruit body as well as sides, externally drying dark brown or dark red-brown, darker over fruit body, densely velutinous on fruit body to densely pilose on wings with trichomes 0.25–1.2 mm, light red-brown or white-yellow, internally drying yellow-white to pale brown on wings contrasting noticeably but not markedly with grayish red-brown fruit body with red-brown rays extending into wings, fruit body 4–6 mm high, wings 6–9 mm high, distance between highest points of 2 wings 0–2 mm, width of mericarp 8–10(11) mm, 1.5–2(–2.5)× height of fruit body, width of fruit body (2)2.5–3(3.5) mm, 1/4–1/3 width of mericarp; seeds 2.25–2.5(3.3) × 1.6–2.25 mm, shiny brown.

Iconography. Krings and Braham (2005: 126, tab. 10.1, fig. A, as *Gouania eurycarpa*); Steyermark and Berry (2004: 476, fig. 402, excl. floral insert, as *G. polygama*); Reissek (1861: tab. 25, fig. 7; tab. 26, fig. 9a, 9b as *G. colurnifolia*). An excellent image of the stipules of *G. velutina* can be viewed at <http://www.tropicos.org/ImageFullView.aspx?imageid=100217678>.

Habitat and distribution. *Gouania velutina* is known from Mexico (Isthmus of Tehuántepec, Oaxaca), northwestern Costa Rica (Guanacaste and Garabito, Puntarenas), northern and central Panama (Chiriquí and Veraguas), northwestern Trinidad, and northern South America (northern Venezuela, Guyana, and northern Brazil). It is found in savannas and dry shrub lands, from elevations of 0 to 500 m in Central America and Mexico, from 0 to 70 m in Trinidad, and from 0 to 1000 (rarely to 1600) m in South America (Figs. 5A, 6A, 8A).

IUCN Red List category. Assessed as Data Deficient (DD) by IUCN (2012) criteria, I have seen 126 collections of *Gouania velutina* from scattered locations from Oaxaca, Mexico, to northern South America. The species has an estimated area of occupancy of at least 336 km^2. However, as this species is only known from vulnerable savannas and dry shrub lands, further study is strongly recommended to determine its conservation status.

Phenology. *Gouania velutina* has been collected in flower in Mexico in August and September, in Costa Rica and Panama in September and November, and in Trinidad in October and November.

Discussion. Specimens of *Gouania velutina* from Mexico, Central America, and Trinidad closely resemble the Brazilian type of *G. colurnifolia*. The type of *G. velutina* from Guyana differs from that of *G. colurnifolia* only in the presence of a few trichomes along the disc annulus. The Mexican and Central American specimens all have the annulus glabrous, but specimens from Trinidad (and South America) can have the annulus either glabrous or pubescent. Material from South America (excluding the types) differs from that in North America by frequently losing the stipules prior to anthesis, in the lower lobe of the stipule being sometimes somewhat smaller, and the coloration pattern of the internal surface of the mericarp more variable. The synonymy employed here was first published by Triana and Planchon (1872: 382).

The names *Gouania velutina* and *G. colurnifolia* have not previously been applied to Central American or Mexican specimens. Specimens of *G. velutina* have been misidentified as either *G. polygama* or *G. eurycarpa* and were treated in Krings and Braham (2005) as the latter. *Gouania polygama* is easily distinguished in fruit by its nearly glabrous, dumbbell-shaped mericarps versus velutinous, butterfly-shaped mericarps in *G. velutina*. In flower, *G. polygama* differs in its rarely retained, bilobed stipules, with both lobes lanceolate, the annulus always pubescent, and the disc lobes (1/3–)2/5–3/5 (–2/3) the length of the sepal lobes versus the bilobed stipules with the lower lobe orbicular to reniform with the margins recurved to the stipule lobe folded in half to cucullate, the usually glabrous annulus, and the disc lobes (1/2–)2/3–1× the sepal length in *G. velutina*. *Gouania eurycarpa* differs from *G. velutina* in both of the lobes of the bilobed stipules lanceolate, the disc lobes square or transversely rectangular, bilobed, and 1/4 to 1/3 the length of the sepals, and the mericarps emarginated to cleft at both apex and base, with the internal surface lacking red-brown rays in the wings. In *G. velutina*, the lower lobe of the stipule is orbicular to reniform with the margins recurved to the stipule lobe folded in half to cucullate, the disc lobes are lanceolate, unlobed, and longer relative to the sepals, and the mericarps emarginate only at the base with red-brown rays extending from fruit body into the wings.

Figure 402 in Steyermark and Berry (2004) is labeled as *Gouania polygama*, but depicts a specimen with pubescent mericarps of the shape and internal markings that better correspond to those of *G. velutina*. Large stipules are shown in the figure, but the actual shape and bilobed nature are not clear. The floral insert of Figure 402 in Steyermark and Berry (2004) represents neither the flower of *G. velutina* nor *G. polygama*. The illustrations cited from Reissek show only the leaves.

Additional specimens examined from Mexico, Central America, and the West Indies. COSTA RICA. **Guanacaste:** Gulf of Nicoya, Island of San Lucas, *Barclay 2758* (BM); Buissons a Nicoya, *Tonduz 13661* (BM, G, GH); halbwegs zwischen Matapalo und Salinas an der Pazifikküste, N Tamarindo, *Döbbeler 2328* (M); S Tamarindo, etwa 1.5 km SW Icacal, *Döbbeler 3828* (M); Tamarindo an der Pazifikküste, Hang kurz östlich oberhalb der "Cabinas Pozo Azul," *Döbbeler 4713* (M); P. N. Santa Rosa, *Barringer et al. 4030* (F, MO), *Liesner 4338* (MO; Fig. 2N), 3–4 km E of park headquarters, *Liesner 2381* (MO); La Cruz, P. N. Guanacaste, Volcán Orosí, Est. Pitilla, Sta. Cecilia 9 km S, *López 82* (K, MO; Fig. 1I); La Cruz, P. N. Santa Rosa, *Janzen 10120* (MO), cuenca del Papagayo, sect. Santa Elena, Tierra Blanca, *González & Espinoza 2622* (MO), cerca de la Est. Murciélago, *Quesada 40* (K, MO, NY), Quebrada de Costa, *Garwood et al. 503* (BM, MO); Liberia, P. N. Santa Rosa, Faja Costeña del Golfo de Papagayo, *Fernández & Hood 1276* (MO), 30 km NW of Liberia, *Janzen 12133* (MO), de Bahía Salinas a Santa Cecilia, Est. Santa Rosa, *Espinoza 972* (MO); Liberia, *Jiménez M. 1561* (NY), Hac. Pocosol, faldas del Volcán Orosí, *Jiménez L. s.n.* [16 dic. 1966] (F); Bagaces, *Quiros C. 856* (F), Comelco E, W of Bagaces, *Heithaus 370* (MO), Guayabo, *Berrocal & J. Sánchez 107* (MO), Comelco, 5 km NW of Bagaces, *Opler 1911* (F, MO); Comelco, near Bagaces, area A, *Opler 447* (F), P. N. Palo Verde, Cuenca del Tempisque, Ojo de Agua, Papayito, Balas de Cañon, *Acosta et al. 2573* (MO), P. N. Palo Verde, Valle del Tempisque, Est. Palo Verde, Cerro Jocote, *Chavarria 901* (F, MO); Cañas, *Daubenmire 559* (F), Finca La Pacífica, *Daubenmire 283* (F); Santa Cruz, R. V. S. bosque Diriá, Cuenca del Tempisque, Fila Vista del Mar, *González 1265* (MO), *Chavarría et al. 1798* (MO). **Puntarenas:** Garabito, Cuenca del Jesús María, *Rodríguez G. et al. 4141* (MO, NY), *Rodríguez G. et al. 1384* (MO), Valle del Tárcoles, Punta Loros y alrededores, *Hammel et al. 18851* (MO). MEXICO. **Oaxaca:** 9 mi. W Zanatepe, *Vaughan et al. 750* (MO); Juchitán, 7 km al W de Almoloya, hacia la Torre de Microondas, Palma Sola, Mpio. del Barrio, *Torres C. & Cabrera C. 6195* (MEXU). PANAMA. **Chiriquí:** Chorcha, *Gutiérrez de S. 33* (MO). **Veraguas:** Santiago, Cerro Forestal, *Rodríguez 46* (F, MO), ca. 5 mi. N Santiago, vic. Santa María river, *Blum & Tyson 613* (MO).

TRINIDAD. s. loc., *Fendler 281* (BM, K), *Othmer s.n.* [4 Nov. 1903] (M), *Lockhart s.n.* [s.d.] (G); Guanapo, *von Eggers 930* (G, M, PR, TEX); ad Caroni, *von Eggers 1378* (US); Biscayne Bay area of Monos Island, *Howard 10402* (A); S Augustine Circular Rd., *Richardson 998* (NY); St. Ann's, *Broadway 5071* (A, BM, F, G, MO); Valley, Hort. Trin., *Broadway 4426* (MICH).

Selected specimens examined from South America. BRAZIL. **Pará:** Forte São Joaquim, Rio Jacutú, *von Luetzelburg 20581* (M). **Paraíba:** Maturéia, Pico do Jabre, *Agra et al. 4019* (MO). **Pernambuco:** s. loc., *Pickel 554* (B); Floresta, Inajá, Res. Biol. Serra Negra, *Rodal & Tamashiro 617* (K). **Roraima:** SEMA Ecol. Stat., Ilha de Maracá, *Ratter et al. 5499* (NY). GUYANA. **East Berbice:** Berbice–Corentyne region, Baba Grant Sawmill, Corentyne River

above Cow Falls, *McDowell & D. Gopaul 2426* (B, NY, TEX, US). **Essequibo:** U. Takutu–U. Essequibo Region, along tributary of Takutu River, *Gillespie & Gopaul 2000* (TEX, US), S Rupununi savanna, *Gillespie et al. 1623* (TEX, US). **Rupununi:** Sand Creek, "Rupununi R.", *Wilson-Browne 101* (K, NY); St. Ignatius, Lethem Rd., Moka-Moka Creek, *Harrison 1330* (K, NY). VENEZUELA. **Anzoátegui:** Libertad, rd. from El Vigia to Buenos Aires, *Davidse & González 19475* (MO, NY). **Bolívar:** Nun. Sifontes, Tumeremo, via Fuerte Tarabay, *Knab-Vispo 1248* (NY); Piar, la Camilera, 40 km O de El Manteco, *Delascio C. & Liesner 7001* (MO, NY); cercanias al Palmar, Minas de Manganeso-Dolomita, *Colella 1552* (NY, TEX); 1 km N of Paragua, *Liesner & González 5764* (MO). **Carabobo:** Maturín, near Las Trincheras, *Alston 5625* (NY); Valencia, *Pittier 9020* (NY). **Guarico:** Est. Biol. de los Llanos, Calabozo, *Ramírez 649* (MO); Río Orituco, *Ramírez 624* (MO); ca. 39 km SSW of Calabozo on Hato Masaguaral, *Rondeau 508* (MO). **Mérida:** Guayana, *Schwabe s.n.* [Aug. 1959] (B). **Portuguesa:** Guanare, UNELLEZ, *Stergios & Aymard 6444* (MO). **Táchira:** Capacho, arriba de Peribeca, hacia El Topón, *Bono 5147* (MO). **Zulia:** Bolívar, carr. El Consejo–Quiroz–El Pensado–Las Mercedes, entre El Pensado y Las Mercedes, *Bunting 5710* (MO); Colón, carr. Casigua–Palmira–Encontrados, *Bunting & Fucci 9815* (NY).

Rejected Name

Gouania paniculata Spreng., Neue Entdeck. Pflanzenk. 3: 49. 1822. TYPE: Hispaniola. "S. Dom.," s.d., *C. L. G. Bertero s.n.* (lectotype, designated here G-DC [G00206175] not seen, G-DC digital image!).

Sprengel (1822) published this name without citing a collector but including the locality of the collection as Hispaniola. A number of the characters described are at odds with *Gouania*, such as the tendrils lacking, the ciliate bracts, and the corolla absent. De Candolle (1825) included this species as *Gouania ? paniculata* and cited a collection in his herbarium, *C. L. G. Bertero s.n.* from Sancto Domingo. I have examined a digital image of this collection (G00206175) and believe it to be an isotype of *G. paniculata*. The *Bertero* collection at G-DC (G00206175) matches the Sprengel (1822) description, and we know that at the time of publication (1822), Sprengel had material of Bertero from Hispaniola because he cites for the first species in this same paper (*Calymperes berterii* Spreng.) a *Bertero* collection from Hispaniola. The G-DC specimen has two labels, but neither appears to be in Sprengel's hand, suggesting that this is probably not the holotype, which was most likely in the Müller-Sprengel herbarium that was purchased by B and is no longer extant. I identify *Bertero s.n.* (G-DC [G00206175]) from the digital image as *Alchornea latifolia* Sw. (Euphorbiaceae) and select it as the lectotype of *G. paniculata*.

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Appendix 1. Index to Exsiccatae. Collections are alphabetical by collector name. The number in parentheses corresponds to the species number in the List of Species. All type collections (including syntypes, isosyntypes, lectotypes, isolectotypes, neotypes, and epitypes) appear in boldface. All collections cited here were examined by the author. Species listed are those found in North America (from Florida and Mexico to Panama and the islands of the Caribbean); the specimens include members of those species found in South America.

List of Species

1. *Gouania colombiana* Suess.
2. *Gouania conzattii* Greenm.
3. *Gouania croatii* A. Pool
4. *Gouania ekmanii* Alain
5. *Gouania eurycarpa* Standl.
6. *Gouania ferruginea* A. Pool
7. *Gouania guiengolensis* A. Pool
8. *Gouania hypoglauca* Standl.
9. *Gouania lupuloides* (L.) Urb.
10. *Gouania obamana* A. Pool
11. *Gouania polygama* (Jacq.) Urb.
12. *Gouania pubidisca* A. Pool
13. *Gouania rosei* Wiggins
14. *Gouania stipularis* DC.
15. *Gouania velutina* Reissek

Abbott, W. 2759 (11), *2823* (9); *Acevedo, D. 92* (8); *Acevedo-Rodríguez, P. 7011* (9); *Acevedo-Rodríguez, P. & A. Reilly 2295* (9); *Acevedo-Rodríguez, P. & A. Siaca 3812* (9), *7087* (9); *Acevedo-Rodríguez, P. et al. 3363* (11), *7139* (11); *Acosta, L. 247* (9), *2149* (1); *Acosta, L. et al. 2573* (15); *Acosta Pérez, R. & G. Castillo C. 962* (9); *Adams, C. 5673* (9), *8156* (9); *Agra, M. F. et al. 4019* (15); *Aguilar, R. 585* (8), *2756* (11), *3276* (8), *3755* (11), *4843* (9), *5735* (1), *8329* (11), *8444* (11); *Aguilar, R. et al. 116* (8); *Aguilar G., J. I. 219* (9), *1127* (9); *Aguilar H., M. 125* (9), *345* (9); *Aguilar M., G. & J. Aguilar M. 4936* (9), *4942* (9); *Aguilar M., G. & S. Aguilar 1304* (9); *Aguilar M., G. & A. Cortés C. 4513* (11), *4534* (9); *Aguilar M., G. & G. López A. 8556* (11), *8674* (11), *8701* (9), *8708* (11), *8771* (11), *9194* (9), *9249* (11); *Aguilar M., G. et al. 4599* (11), *4662* (9), *4912* (9), *5208* (11), *5353* (9), *8147* (11), *8811* (11), *8952* (11); *Aguilar Zepeda, J. 388* (9); *Alavez Solano, D. s.n.* [s.d.] (11); *Alcorn, J. 1941* (9), *2002* (11), *2217* (11); *Alfaro, E. 1838* (9), *2478* (9); *Allard, H. 13199* (11), *13200* (9), *13222* (11), *13413* (9), *13458* (11), *14470* (11), *16617* (11), *18078* (11); *Allen, P. H. 103* (11), *1078* (11), *2863* (11), *4108* (11), *4290* (11), *5441* (11); *Alston, A. H. G. 5625* (15); *Alvarado-Cárdenas, L. O. & A. Reyes-García 745* (12); *Alvarado-Cárdenas, L. O. et al. 466* (11); *Alvarado Flores, F. 97* (9); *Álvarez M., D. 388* (5), *455* (5), *629* (5), *7749* (5); *Álvarez M., D. & J. P. Abascal 2838* (5), *3006* (11); *Álvarez M., D. & I. Jiménez 7702* (5); *Álvarez M., D. & C. Jimenez J. 3033* (5), *3278* (5), *3602* (5); *Álvarez M., D. et al. 6822* (11), *7063* (11); *Ames, O. s.n.* [11 Nov. 1902] (11); *Ancuash Atsut, E. 327* (11), *1229* (11), *1501* (11); *Anderson, A. s.n.* [s.d.] (9); *Anderson, W. & C. W. Laskowski 3688* (9); *Andrade S., A. 86* (13); *Angulo, L. 571* (11); *Ankli, A. AANK376* (9); *Aquino, A. 202AA* (9), *207AA* (12), *211AA* (9); *Araquistain, M. 412* (11), *3140* (8), *3169* (8); *Araquistain, M. & D. Castro C. 1835* (11); *Araquistain, M. & P. P. Moreno 991* (11); *Araya, F. 52* (8); *Araya, F. & J. F. Corrales 795* (8); *Aristeguieta, L. 5138* (15); *Arnason, J. & J. Lambert 17886* (11), *17918* (5); *Arroyo Padilla, L. 1351* (11); *Arvigo, R. & P. Cocom 696* (11), *703* (5), *716* (11); *Arvigo, R. et al. 72* (9), *733* (9); *Atha, D. & T. A. Zanoni 752* (11), *877* (9); *Avendaño R., S. 679a* (9); *Ayala, M. G. 204* (13), *1121* (13), *1232* (14); *Ayala Flores, F. 2903* (11); *Aymard, G. 4285* (11); *Aymard, G. et al. 2340* (15), *10158* (11); *Azofeifa, A. 671* (11).

Bacab W., G. 150 (5); *Bailey, L. 257* (11); ***Baker, C. F. 152 (673)*** (12), *1885* (11); *Baker, C. F. & M. Arbarca y Vascquez 3895* (11); *Baker, M. A. 6836* (1); *Baker, R. 14246* (11); *Balam, F. 627* (5); *Baldwin, A. 52* (9); *Balick, M. J. et al. 2121* (5); *3016* (11), *3197* (11), *3612* (10); *Bang, M. 1187* (11), *1270* (11); *Barclay, G. W. 1011* (11), *2665* (12), *2758* (15); *Barco Rodríguez, M. MABR-170* (9); *Barkley, F. & E. D. Barkley 39672* (11); *Barkley, F. & G. Gutiérrez V. 1797* (11); *Barquero M., H. s.n.* [Aug. 1969] (8); *Barreto, H. 7090* (11); *Barringer, K. et al. 4030* (15), *4059* (8); *Bartholomew, B. M. et al. 2606* (9), *3499* (9); *Bartlett, H. H. 11433* (9), *11564* (9), *11951* (9); *Bates, W. s.n.* [s.d.] (9); *Beaman, J. 5217* (9); *Beard, P. 1328* (11); *Beetle, A. 2120* (11); *Bélanger, C. 316* (9), *624* (9); *Bello C., E. & E. Cruz L. 5392* (11); *Belshaw, C. M. 3198* (11); *Benitez-Paredes, A. 3890* (9); *Bensman, R. 298* (1); *Berlandier, J. 2204* (9); *Berlin, B. 794* (1), *861* (1); *Bernardi, L. 2587* (11); *Bernoulli, K. G. 1180* (11); *Bernoulli, K. G. & O. R. Cario 2048* (11); *Berrocal, J. & J. Sánchez 107* (15); ***Bertero, C. L. G.*** *s.n.* [1816–1821] (9), ***s.n.*** [s.d.] (11); *Billiet, F. & B. Jadin 6823* (11); *Biolley, P. 7107* (9); *Blackmore, S. & G. L. A. Heath 1709* (11), *1803* (9); *Blanchet, J. 3054* (11), *3104* (15); *Blandón, L. 105* (9); *Blodgett, F. H. s.n.* [s.d.] (9); *Blum, K. E. 2041* (11); *Blum, K. E. & J. D. Dwyer 2116* (11); *Blum, K. E. & E. L. Tyson 613* (15); *Boege, L. 627* (13); *Boldingh, I. 2811* (9); *Bono, J. 4634* (11), *4972* (15), *5147* (15); *Boom, B. M. 10030* (9); *Botello, D. 22* (11); *Bourdy, G. 1547* (11); *Bourgeau, E. 1464* (11), *1743* (9), *1745* (9); *Box, H. E. 1228* (9), *1856* (9); *Brace, L. 157* (9), *386* (9), *387* (9); *Brandegee, T. S. s.n.* [10 Oct. 1904] (13); *Bravo Hollis, H. 352* (9), *1310* (11); *Breckon, G. J. et al. 1094* (13), *1202* (11); *Breedlove, D. E. 7636* (11), *18978* (11), *19832* (9), *20302* (9), *23063* (9), *28108* (11), *28466* (9), *28594* (12), *29054* (9), *29146* (9), *29310* (11), *36724* (12), *37198* (11), *37404* (9), *48634* (11), *49118* (11), *53632* (9), *53648* (9); *Breedlove, D. E. & D. I. Axelrod 43216* (13); *Breedlove, D. E. & G. Davidse 54431* (9); *Breedlove, D. E. & P. H. Raven 13541* (9); *Breedlove, D. E. & R. F. Thorne 20726* (11), *21055* (11); *Brenes, A. s.n.* [6 Nov. 1932] (11), *6414* (11), *11827* (11); *Breteler, F. J. 4408* (11); *Bretting, P. K. J-82* (9), *J-87* (9); *Brewer, S. 5133* (11); *Briceño, E. & J. Rosales 158* (15); *Britton, E. G. 12* (11), *6537* (9), *Britton, N. L. 361* (9), *636* (9), *7170* (9), *15261* (9); *Britton, N. L. & E. G. Britton 8852* (9); *Britton, N. L. & J. A. Shafer 327* (9); *Britton, N. L. & P. Wilson 356* (11); *Britton, N. L. et al. 103* (11), *106* (11), *170* (9), *1147* (11); *Broadway, W. E. s.n.* [Dec. 1904] (9), *1200* (11), *3418* (11), *3995* (11), *4410* (11), *4426* (15), *5071* (15), *9115* (11); *Brokaw, N. V. L. & M. Schulze 122* (5), *194* (5); *Brumbach, W. 9528* (9), *9537* (9); *Buch, W. 1232* (9); *Bullock, S. H. 1198* (13), *1233* (13), *1382* (13); *Bunting, G. S. 5710* (15), *6724* (11); *Bunting, G. S. & L. Alfonso G. 8034* (15); *Bunting, G. S. & M. Fucci 8421* (15), *8423* (15), *9815* (15), *9817* (15); *Bunting, G. S. & L. Licht 600* (11), *1068* (11); *Bunting, G. S. & A. Stoddart 8994* (11); *Bunting, G. S. et al. 12267* (11); *Burch, D. et al. 1395* (11); *Burchell, W. 8756* (15); *Burger, W. C. & R. L. Liesner 6666* (11), *6918* (11);

Burger, W. C. & G. Mata U. 4629 (9); *Burnham, R. 41* (11), *1391* (1); *Burnham, R. & A. Krings 1571* (1); *Busey, P. 355* (11), *484* (11); *Bye, R. A. 2902* (9), *3209* (9), *3238* (9), *5681* (9), *5950* (9), *8845* (9); *Bye, R. A. et al. 18021* (9).

Caballero, R. 50 (11); *Cabrera C., E. F. 15276* (9), *16991* (5); *Cabrera C., E. F. & H. de Cabrera 2284* (9), *3692* (11), *3969* (5), *6209* (11), *6262* (5), *7387* (7), *7808* (5), *9297* (9), *9401* (9), *9460* (9), *9511* (9), *9571* (9), *9580* (9), *9716* (9), *9870* (5), *10135* (9), *10583* (5), *12318* (11), *12556* (5), *12983* (5), *15195* (9); *Cabrera C., E. F. & L. Cortés A. 73* (5), *101* (5), *195* (5), *237* (5), *260* (9), *352* (5); *Cabrera C., E. F. & G. Durán 433* (5), *610* (5), *666* (5); *Cabrera C., E. F. & M. J. Huft 7463* (9); *Cabrera C., E. F. & G. Ibarra Manríquez 1187* (5), *1443* (5); *Cabrera C., E. F. & R. Torres C. 915* (5), *1030* (5), *1070* (5); *Cabrera C., E. F. & S. Zárate P. 1552* (5); *Cabrera C., E. F. et al. 7733* (9), *7758* (11), *9762* (5); *Calderón, S. 150* (11), *150a* (9), *1256* (9), *1548* (9); *Calderón Vásquez, R. s.n. ISF00724* (9); *Callejas, R. et al. 4555* (1); *Calónico S., J. 4741* (13), *17920* (9), *18283* (14); *Calónico S., J. et al. 4228* (13), *5838* (13), *21341* (11), *21428* (9), *22225* (11), *24979* (11); *Calzada, J. I. 104* (10), *948* (9), *1684* (9), *2899* (11), *8347* (11), *14202* (11), *14518* (9); *Calzada, J. I. & J. Arellano 2241* (9); *Calzada, J. I. & I. Espejel 6675* (9); *Calzada, J. I. et al. 3970* (9), *6430* (9), *6664* (9); *Cámbar, I. 84* (9); *Campbell, E. J. F. 76* (10); *Campos, J. 6156* (11); *Campos, J. & M. Vásquez T. 2546* (11); *Campos V., A. 3345* (9), *5236* (10); *Campos V., A. et al. 62* (11); *Canela Lazaro, M. s.n.* [8 Oct. 1938] (9); *Cantrall, I. J. 2* (5); *Cárdenas, D. 1174* (3), *2054* (3); *Cárdenas C., C. 93* (11); *Carleton, M. 442* (10); *Carlson, M. s.n.* [1946] (9); *Carnevali, G. 4980* (5); *Carnevali, G. & F. May-Pat 5933* (9); *Carnevali, G. et al. 4303* (9), *6462* (9); *Carrasquilla, L. & R. Mendoza 1163* (11); *Carrasquillo, J. A. 117* (9); *Carrillo-Reyes, P. 5546* (2); *Carruthers, W. et al. s.n.* [Nov. 1884] (9); *Carter, A. M. & F. Chisaki 3468* (13), *3590* (13); *Carter, R. & R. G. García 5318* (9); *Carvajal, E. 81* (9); *Carvajal V., A. 283* (11), *322* (11), *406* (11); *Cascante, A. 546* (8), *782* (9), *1245* (11); *Cascante, A. & M. A. Blanco 967* (11); *Castillo, S. s.n. ISF00434* (9), *s.n. ISF00717* (9), *s.n. ISF00731* (9); *Castillo Mont, J. J. & J. A. Castillo Mont 1639* (11); *Castillo Mont, J. J. & M. Véliz Pérez 2775* (6); *Castrejón R., J. F. et al. 698* (9), *976* (13); *Castro C., D. 2311* (9), *2352* (9), *2411* (11); *Catalán H., C. 184* (9); *Catalán H., C. & F. Terán C. 853* (9); *Catesby, M. et al. s.n.* [1726] (9); *Cedillo T., R. 2624* (10), *2913* (9), *3450* (11), *3467* (11), *3528* (11); *Cedillo T., R. & J. I. Calzada 176* (10); *Cedillo T., R. & R. Torres C. 1036* (9); *Centeno, C. 190* (11), *211* (11); *Chacón G., A. 718* (11); *Chacón G., I. A. 440* (11), *964* (8); *Chan V., C. 4245* (9), *4477* (5), *4573* (5), *6094* (5); *Chapman, A. s.n.* [s.d.] (9); *Charlton, D. et al. 2818* (13); *Chavarría, U. 324* (11), *867* (11), *901* (15), *1790* (9); *Chavarría, U. et al. 1798* (15); *Chavelas Pólito, J. ES-4273A* (11); *Chavelas Pólito, J. & A. Pérez J. 312* (11); *Chavelas Pólito, J. et al. 2097* (11); *Chaves, J. L. 539* (8); *Chávez, L. s.n.* [6 Oct. 1997] (9); *Chiang C., F. 188* (9), *230* (9), *485* (11); *Chiang C., F. & G. Flores F. 1069* (14); *Chinchilla P., F. s.n. ISB00664* (9), *s.n. ISB00696* (12); *Cicero, J. 8310* (9); *Cid Ferreira, C. 4706* (15); *Clarke, O. et al. 1589-12* (9); *Claussen, P. s.n.* [s.d.] (11); *Clement, (Brother) 224* (11), *3136* (11), *7445* (9); *Clement, E. et al. TB93/177* (11); *Clewell, A. F. & G. Cruz 4106* (11); *Cochrane, T. S. et al. 12294* (14); *Colella, M. 1049* (15), *1552* (15); *Combs, R. s.n.* [s.d.] (11), *93* (11); *Comision de Dioscorea P192* (11); *Contreras, E. 300* (5), *368* (5), *1581* (5), *3115* (11), *3459* (11), *3675* (11), *5571* (5), *5591* (11), *6456* (11), *7433* (11), *7547* (9), *9313* (11), *9450* (10), *9498* (10), *11148* (10); ***Conzatti, C.*** *s.n.* [9 June 1907] (2), *827* (11), ***1567*** (2), *1829* (2), *1935* (2), *4402* (12), *4407* (12), *4902* (2); *Cook, M. et al. 93* (11); *Cooper, G. 162* (11); *Cordero, G. 113* (11); *Coronado G., I. & J. Reyes 6462* (12), *6510* (11); *Coronado G., I. & R. M. Rueda 3516* (9); *Coronado G., I. et al. 470* (11), *1546* (11), *3094* (11); *Correa A., M. D. 498* (11); *Correa A., M. D. & R. L. Dressler 986* (8); *Correa A., M. D. et al. 3443* (11), *3816* (11), *8339* (11); *Correll, D. S. 42156* (9), *44193* (9), *50213* (9), *51129* (9); *Correll, D. S. & H. B. Correll 47621* (9); *Correll, D. S. et al. 40277* (9), *51075* (9); *Cortés A., L. 57* (11); *Cortés A., L. & R. Torres C. 104* (9), *1040* (11); *Cortés A., L. et al. 212* (11), *267* (9), *490* (9), *640* (9), *771* (9); *Cowan, C. 2025* (9), *2594* (11), *2799* (9); *Cowan, C. et al. 2549* (11); *Cowell, J. F. 79* (11); *Crane, C. 581* (5); *Croat, T. B. 4622* (11), *4709* (11), *4825* (11), *5744* (11), *7075* (11), *7105* (11), *7154* (11), *7235* (11), *7274* (3), *7723a* (11), *7769* (11), *7984* (3), *8584* (11), *8668* (11), *10852* (11), *12651* (11), *12682A* (11), *12699* (3), *12739* (3), *12894A* (11), *13005* (11), *13120* (11), *13482* (3), *13673* (9), *15020* (11), *17946* (11), *21902* (11), *26764* (9), *35776a* (8), *41935* (9), *42152* (9), *45467* (2), *58834* (1), *67750* (9), *69869* (11), *78530* (9); *Croat, T. B. & D. P. Hannon 63191* (11), *64065* (11), *64498* (9), *64650* (9); *Croat, T. B. & P. Díaz Jiménez 100142* (11), *100318* (9); *Croat, T. B. & M. Sizemore 81631* (11); *Croizat, L. 1017* (11); *Crutchfield, J. & M. C. Johnston 5701* (9); *Cuadros, H. 3285* (11); *Cubas, H. 59* (9); *Cuevas G., R. & N. Nuñez 3987* (9); *Curran, H. M. s.n.* [4 Dec. 1952] (11), *s.n.* [28 Dec. 1952] (11), *37* (15), *198* (15); *Curtiss, A. 38* (9), *272* (11), *474* (9); *Czerwenka, J. & S. Peláez F. 415* (9).

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A TAXONOMIC REVISION OF *DOMBEYA* SECT. *DECASTEMON* (MALVACEAE)[1]

Wendy L. Applequist[2]

ABSTRACT

Dombeya Cav. (Malvaceae) as presently defined encompasses over 200 species and considerable morphological variation. Within the 2- to 3-carpellate *Dombeya* subg. *Xeropetalum* (Delile) K. Schum., almost half of the recognized species belong to *Dombeya* sect. *Decastemon* Planch., which is endemic to Madagascar and traditionally distinguished by its umbellate rather than cymose inflorescences. The most recent taxonomic treatment of this section recognized 47 species and numerous infraspecific taxa; an additional species referable to this group was recently described. The present treatment recognizes 41 species and 11 subspecies. Six species (*D. micrantha* Appleq., *D. milleri* Appleq. & Bosser, *D. pauciflora* Appleq., *D. pilosissima* Appleq. & T. Andriam., *D. ratovosonii* Appleq. & Bosser, *D. vohemarensis* Appleq.) are newly described, and one (*D. ramiovensis* (Arènes) Appleq. [≡ *D. farafanganica* Arènes subsp. *ramiovensis* Arènes]) is newly elevated to specific rank. *Dombeya parvipetala* Arènes, which (like *D. pilosissima*) has a small, dichotomously branching cymose inflorescence, is transferred from *Dombeya* sect. *Xeropetalum* (Delile) Planch. to *Dombeya* sect. *Decastemon*. The following names are transferred: *D. ambalabeensis* Arènes subsp. *analavelonae* (Arènes) Appleq. [≡ *D. analavelonae* Arènes], *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq. [≡ *D. farafanganica*], *D. decanthera* subsp. *latipetala* (Arènes) Appleq. [≡ *D. farafanganica* subvar. *latipetala* Arènes], *D. subviscosa* Hochr. subsp. *ihosyensis* (Arènes) Appleq. [≡ *D. ambongensis* Arènes var. *ihosyensis* Arènes], *D. subviscosa* subsp. *sakarahae* (Arènes) Appleq. [≡ *D. ambongensis* subsp. *sakarahae* Arènes]. Subsections formerly recognized are not reliably separable by morphology, so only six series are recognized, one of them newly described (*Dombeya* ser. *Pentandrae* Appleq.) and one newly recognized at that rank [*Dombeya* ser. *Decantherae* (Arènes) Appleq.]. Placement of species into series has been greatly rearranged, although some series remain heterogeneous and are used for convenience with no assertion of probable monophyly. Consistent with published reports of hybridization in other subgroups of *Dombeya*, a number of probable hybrid specimens are noted, several of readily identifiable parentage, but are not nomenclaturally recognized.

Key words: *Decastemon*, *Dombeya*, Madagascar, Malvaceae, Sterculiaceae.

Dombeya Cav. (Malvaceae, formerly Sterculiaceae) is a woody genus native to Madagascar, the Mascarenes and Comoros, and Africa extending into the Arabian Peninsula. According to the most recent treatments, the genus includes close to 230 species; Madagascar, with almost 200 species, is the primary center of diversity. As presently circumscribed, *Dombeya* encompasses enormous variation in leaf

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and floral morphology; subgenera are defined by the possession of two or three (four) vs. five carpels. A number of smaller genera endemic to Madagascar and the Mascarenes have obvious affinities to *Dombeya* (e.g., *Helmiopsis* H. Perrier, *Trochetia* DC., *Ruizia* Cav.). Published molecular data strongly suggest that *Dombeya* is paraphyletic due to the exclusion of some of these (Le Péchon et al., 2010; Skema, 2012), even after the exclusion of an outlying lineage as *Andringitra* Skema (Skema, 2012).

Dombeya is an important component of the flora in Madagascar in terms of its range and number of species; it is found in most of the island's diverse habitat types, and many narrowly endemic species are known. While the African species were recently revised by Seyani (1991) and the Mascarene species by Friedmann (1987), the last treatment of *Dombeya* in Madagascar (Arènes, 1958, 1959) is now obsolete. Far more herbarium material has become available since these publications, including collections of a number of new species that were not seen by Arènes. Species delimitations that were made using very limited material are sometimes questionable, which may have significant negative consequences for conservation activities and decision-making (Bortolus, 2008), and botanists in Madagascar have found reliable identification of specimens using the existing literature to be difficult. An updated taxonomic treatment of this genus in Madagascar is, therefore, urgently needed.

As a step toward that goal, this paper presents a revision of *Dombeya* sect. *Decastemon* Planch., which is endemic to Madagascar and is characterized by the combination of 2- to 3- (to 4)-carpellate ovaries and, traditionally, umbellate inflorescences. The treatments of this section by Arènes (1958, 1959) recognized 47 species, as well as 13 subspecies, 14 varieties, two subvarieties, and one form. It is the opinion of the present author that Arènes was too strongly inclined toward splitting when the affinities of atypical specimens were uncertain. Hence, the number of species recognized is herein reduced to 41 (of which six are newly described) via the placement of a number of names, especially at infraspecific ranks, into synonymy. Eleven subspecies are also recognized.

Taxonomic History

The taxonomic history of *Dombeya* begins with Cavanilles' publication of the genus name (1786) and 11 species (1787). These included several species of the present *Dombeya* subg. *Dombeya* and *D. decanthera* Cav., the first published species referable to *Dombeya* sect. *Decastemon*; thus, the initial circumscription already included considerable morphological heterogeneity. Early authors (including Cavanilles [1786] himself, who simultaneously published *Dombeya* and *Assonia* Cav.) described a number of small genera, now synonymized with *Dombeya*, that did not involve species of *Dombeya* sect. *Decastemon*. The first infrageneric classification was published by Planchon (1850: 225), who subdivided *Dombeya* as then circumscribed into five sections: section *Eudombeya* Planch., section *Dombeyastrum* Planch., section *Pachythyrsus* Planch., section *Xeropetalum* (Delile) Planch., and section *Decastemon*, remarking of the last: "An genus proprium?" All species in the former three sections are referable to the present *Dombeya* subg. *Dombeya*, and specifically to *Dombeya* sect. *Dombeya*; the latter two sections are still recognized and, as presently defined, encompass the large majority of species within *Dombeya* subg. *Xeropetalum* (Delile) K. Schum. *Dombeya decanthera* was the only species included by Planchon in *Dombeya* sect. *Decastemon*, hence the type of the section. Baillon (1885a) published *Dombeya* sect. *Dombeyella* Baill., likewise containing only *Melhania decanthera* (Cav.) DC., i.e., *D. decanthera*; this section name is, therefore, nomenclaturally superfluous and illegitimate under Article 52 of the International Code of Nomenclature (ICN; McNeill et al., 2012). Less than a month later, he published two further species referable to this section in a list of *Dombeya* species that did not include sectional attributions (Baillon, 1885b).

In treating African species of *Dombeya*, Schumann (1900) recognized two subgenera, *Dombeya* subg. *Eudombeya* K. Schum. (a name not allowed under Art. 21.3 of the ICN [McNeill et al., 2012]; [= *Dombeya* subg. *Dombeya*]) and *Dombeya* subg. *Xeropetalum*, formally distinguished by having five versus two or three (rarely four) carpels. These subgenera also display different inflorescence morphologies and inconsistent but conspicuous trends in vegetative features, so that most species can immediately be identified to subgenus without observing the gynoecium; however, it is possible that neither is monophyletic relative to the other (Skema, 2012). Later authors have consistently followed this division. The next major treatment of Malagasy species was by Hochreutiner (1926), who recognized two sections within *Dombeya* subg. *Xeropetalum*, *Dombeya* sect. *Paradombeyastrum* Hochr., and *Dombeya* sect. *Paratrochetiella* Hochr., corresponding to *Dombeya* sect. *Decastemon* and *Dombeya* sect. *Xeropetalum*, respectively. *Dombeya* sect. *Paradombeyastrum* was superfluous and illegitimate due to the inclusion of *D. decanthera*; *Dombeya* sect. *Para-*

Table 1. Arènes' infrasectional classification of *Dombeya* sect. *Decastemon* Planch. All subgroup names were authored by Arènes (1958), and the number of included species follows his treatment.

Subgroup	Defining character(s)	Number of species
subsect. *Longipedicellatae*	peduncle ≤ pedicels	
ser. *Squamigerae*	ovary lepidote	1
ser. *Selinala*	ovary stellate	
subser. *Merika*	petals narrow, petioles glabrous	5
subser. *Digynae*	petals narrow, at least young petioles stellate	9
subser. *Decaryanae*	petals suborbicular	4
ser. *Valafotsy*	ovary glabrous	
subser. *Sely*	pedicels stellate	3
subser. *Mafimafy*	pedicels glabrous or glabrescent	9
subsect. *Decantherae*	peduncle ≥ pedicels	
ser. *Lepidotae*	ovary lepidote	1
ser. *Mananarenses*	ovary stellate	
subser. *Australes*	pedicels glabrous or glabrescent	4
subser. *Lavasoenses*	pedicels stellate	8
ser. *Apikyenses*	ovary glabrous	3

trochetiella was legitimate because the African type of *Dombeya* sect. *Xeropetalum* (*Xeropetalum quinquesetum* Delile [≡ *D. quinqueseta* (Delile) Exell]) was not included. Hochreutiner recognized 12 species in the section corresponding to section *Decastemon*, seven of them newly described, in addition to four varieties.

Arènes (1958, 1959) provided the next, and until now the most recent, complete treatment of *Dombeya* sect. *Decastemon*. He recognized 47 species, 37 of them newly described, as well as numerous infraspecific taxa. His elaborate infrasectional classification (Table 1) divided the section first into two subsections, *Dombeya* subsect. *Longipedicellatae* Arènes and *Dombeya* subsect. *Decantherae* Arènes, based on whether the peduncles were mostly shorter or mostly longer than the pedicels. Within each subsection, a triad of series was defined by ovary indument (stellate, glabrous, or lepidote, the last state being rare in both subsections). In three of the resulting series, two or three subseries were recognized based on variation in petiole or pedicel indument and, in one, petal shape. Types of subgroups were not specified, but in all cases where more than one species was included within a series or subseries, the epithet was derived from the epithet of an included species, which thereby automatically becomes the type, following Article 22.6 of the ICN (McNeill et al., 2012).

Most recently, Skema and Dorr (2010) described a very distinctive new species, *Dombeya gautieri* Dorr & Skema, without specifying its infrageneric placement. This and two related species described in this paper are, based on inflorescence and leaf morphology, best placed in *Dombeya* sect. *Decastemon*.

Circumscription of *Dombeya* sect. *Decastemon* and Infrasectional Classification

Dombeya sect. *Decastemon* has been a morphologically well-defined group, easily recognized by its delicate umbellate inflorescences, in contrast to the cymose inflorescences of *Dombeya* sect. *Xeropetalum*. The present revision complicates this picture by transferring *D. parvipetala* Arènes from *Dombeya* sect. *Xeropetalum* into *Dombeya* sect. *Decastemon* and by placing the newly described *D. pilosissima* Appleq. & T. Andriam. into that section. Both species have few-flowered, relatively symmetrical cymes, whereas the inflorescences of *Dombeya* sect. *Xeropetalum* are usually more asymmetrically branched and often many-flowered, and each has other morphological features that suggest affinities with specific subgroups of *Dombeya* sect. *Decastemon*. In addition, the inclusion of *D. gautieri* and two related species with five short, oppositisepalous fertile stamens substantially increases the range of floral morphology represented within the section.

Molecular data do not suffice to confirm the monophyly of the section, much less of any infrasectional groups. The study by Le Péchon et al. (2010) provides no information on relationships within *Dombeya* sect. *Decastemon*. Skema (2012) included six accessions from five species of *Dombeya* sect. *Decastemon* in a phylogeny within which the section appeared to be polyphyletic. However, her topology was for the most part weakly supported and somewhat problematic: one of the better-supported results relevant to this group placed one collection of *D. australis* Scott-Elliot as sister to *D. farafanganica* Arènes [= *D. decanthera*] rather than to a second collection of *D. australis*. It is worth noting that one of

Table 2. Infrasectional classification within *Dombeya* sect. *Decastemon* Planch. and included species groupings as accepted herein.

Series	Species included therein
I. *Dombeya* ser. *Apikyenses* (4 species)	*D. apikyensis*, *D. aquifoliopsis*, *D. midongyensis*, *D. ramiovensis*
II. *Dombeya* ser. *Decantherae* (2 species)	*D. decanthera* (3 subspecies), *D. lavasoensis*
III. *Dombeya* ser. *Mananarenses* (7 species)	*D. australis* (2 subspecies), *D. capuroniana*, *D. mananarensis*, *D. mandenensis*, *D. mangorensis*, *D. ranofotsyensis*, *D. rariflora*
IV. *Dombeya* ser. *Pentandrae* (3 species)	*D. gautieri*, *D. milleri*, *D. ratovosonii*
V. *Dombeya* ser. *Selinala* (13 species)	*D. ambalabeensis* (3 subspecies), *D. ambohitrensis*, *D. anakaensis*, *D. danguyi*, *D. digyna*, *D. micrantha*, *D. parvipetala*, *D. sakamaliensis*, *D. selinala*, *D. sely*, *D. subviscosa* (3 subspecies), *D. tulearensis*, *D. vohemarensis*
VI. *Dombeya* ser. *Squamigerae* (11 species)	*D. andrahomanensis*, *D. decaryana*, *D. lecomtei*, *D. lecomteopsis*, *D. longipedicellata*, *D. merika*, *D. pauciflora*, *D. seyrigiana*, *D. tavia*, *D. tsiandrensis*, *D. tubulosoviscosa*

two species of *Dombeya* sect. *Decastemon* that the study suggested to be sister lineages to the remainder of *Dombeya* s. str. is the very distinctive *D. gautieri*. However, the other is *D. mandenensis* Arènes, which in its morphology seems to show clear affinities with the "derived" *D. australis* and related species. Molecular data strong enough and including sufficient species to support a major phylogenetically based reclassification of *Dombeya* subg. *Xeropetalum*, therefore, do not exist. Further, sequence data will not be available in the near future from many taxa that are known from only one or a few older collections, including some entire groups of species.

Infrasectional classification is highly desirable for the sake of convenience, given the number of species involved and the complexity of morphological variation, but the question of how to do this is a difficult one. Arènes' (1958) classification is essentially artificial, with groups based largely on single characters that are known to vary homoplasiously within the genus, and hence is of little predictive value. Worse, as can be seen from the greater amount of herbarium material available today, those characters are not entirely reliable for specimen identification. Notably, the types of the glabrous-ovaried *Dombeya* ser. *Valafotsy* Arènes and the stellate-ovaried *Dombeya* ser. *Selinala* Arènes are referable to the same variable species, *D. selinala* Arènes. A distinctive group of species with similar petal morphology is scattered among both series, along with other species that do not belong to that group. Hence, some alteration of infrasectional classification is plainly necessary. However, the extent and pattern of variation within this section (and the entire genus) make it impossible to have confidence in the monophyly of most morphologically defined groups.

Under these circumstances, a relatively simple classification, i.e., dividing the section into series each containing a manageable range of morphological variation, seems preferable. These series may be useful for identification of specimens but are not asserted to be monophyletic as herein circumscribed (summarized in Table 2). A proliferation of ranks should be avoided, as a complicated hierarchical classification implies opinions regarding evolutionary relationships that cannot be supported. The circumscriptions of Arènes' two subsections are strongly correlated with habitat preferences, but there is not one morphological character that reliably separates them (peduncle and pedicel length being too variable within some species to allow specimens to be keyed out consistently). Thus, the subsections are of no practical utility and are not herein recognized.

Morphology

Potentially informative vegetative characters include leaf shape, relative petiole length, leaf venation, the presence or absence of domatia, and the indument of the twigs, leaves, and petiole. The shape of the leaf, including the base and apex, often varies to a certain degree within species; however, certain subgroups are characterized by having leaves usually broadest below or above the midpoint, in either case often tending toward elliptical or oblong-elliptical in some species. In all but one species, small glands are borne in the leaf margins. Secondary venation is usually best described as semicraspedodromous (following the terminology recommended by Ellis et al. [2009]), with veins usually weakening greatly before the margin, a branch or the vein itself terminating at a leaf gland, and lateral branches connecting to neighboring secondary veins by an irregularly reticulated network. There are a few exceptions; notably, three species have genuinely reticulodromous venation on much or all of the leaf. The number of basal and secondary veins can be

useful characters, although the latter in particular is quite variable. The venation is always visible on the abaxial leaf surface, though it is occasionally quite weak or unusually prominent; it is usually visible on the adaxial surface as well, but in a few species is inconspicuous or barely visible. Leaf margins are usually somewhat toothed or wavy; the glands may project slightly or may be borne consistently in the apices of larger teeth, or may be variably placed between teeth or in concave portions of the margin. Very rarely, leaf glands may be entirely absent. Domatia, previously reported from very few species of *Dombeya* (Arènes, 1958; Seyani, 1991), are very common in two series, while being rare or absent in others; unfortunately, their presence is usually not ubiquitous in those species for which substantial material is available, complicating their use for identification.

Vegetative parts may be glabrous or bear stellate trichomes, fimbriate-lepidote scales, small irregular scales, pale or reddish papillae, long unbranched hairs, or very small papillae that sometimes co-occur with stellate trichomes. Indument is sometimes consistent within species, sometimes highly variable. Two-dimensional, short-fimbriate lepidote scales and highly three-dimensional multibranched stellate trichomes may be seen as the extremes of a continuous range of variation that includes a wide variety of intermediates that can be difficult to characterize. Commonly seen forms include long-fimbriate scales and morphologies here termed "scaly stellate" (usually with a well-developed center and relatively short, irregularly three-dimensional or somewhat flattened arms) and "flat-stellate" (a small stellate hair, with most of the diameter consisting of a single rank of fine arms that radiate perpendicular to the leaf surface). Though no one species displays both fully lepidote and fully stellate indument, it is frequent for a single species to display more than one intermediate, and scaly stellate indument can often be viewed as either lepidote or stellate, depending on minor individual variations and viewer expectations.

Stipules, usually small and caducous, are occasionally long and/or persistent. Stipule size can be highly variable within species, perhaps being longer on main twigs than on short side shoots (Skema & Dorr, 2010), but for many species herbarium material is inadequate to determine the natural range of variation, as stipules do not persist on fertile specimens with mature leaves. In most of the species formerly placed in *Dombeya* subsect. *Decantherae*, the stipule base is thickened dorsiventrally and sometimes broadened as well and leaves a stipule scar that is broad and sometimes long, usually broadly hemielliptical to irregularly crescent-shaped, often pale with a spongy or fleshy appearance and often prominently raised at the margins; this character is correlated with leaf morphological characters and is useful in the circumscription of series. Because stipule scars in many species of the cymose-inflorescenced *Dombeya* sect. *Xeropetalum* are also at least slightly broadened and often slightly prominent, this may be the primitive state within *Dombeya* subg. *Xeropetalum* as a whole, though it is developed to an extreme degree in some species of *Dombeya* ser. *Mananarenses* Arènes as herein circumscribed. The inconspicuous linear or narrowly elliptical stipule scars of most species in four series are hypothesized to represent a derived condition.

Relative lengths of the peduncle and pedicels have been considered a critical character in this group, and most species indeed reliably have peduncles that are either distinctly shorter or distinctly longer than the pedicels; further, otherwise relatively cohesive groups of species tend to share the same character state. However, some species have peduncles and pedicels that are, at least sometimes, of relatively similar average length, so that peduncles both longer and shorter than the pedicels may be seen in different individuals or in different inflorescences of the same individual; in a few normally long-peduncled species, very short peduncles occur as an occasional aberration. Arènes (1958, 1959) placed a few such species within *Dombeya* subsect. *Decantherae*, which was putatively defined by the character of long peduncles, along with one species with consistently short peduncles and pedicels (*D. rariflora* Arènes) and another with solitary flowers that have moderately long pedicels and no peduncles (*D. lavasoensis* Arènes). Though those decisions were largely justified by the overall morphology of the included species, it is clear that despite the undeniable usefulness of the character of inflorescence proportion, it cannot be employed as the sole factor defining a subgroup.

Although the inflorescence normally appears umbellate except in *Dombeya parvipetala* and *D. pilosissima*, very short basal branching that makes the inflorescence an umbelliform cyme is seen at least as an aberration in some species; material is sometimes too limited to determine whether this feature is typical for a species. Other variable inflorescence characters include number of flowers, indument, and the shape, persistence, and position of bracteoles. All are too variable to be useful in defining subgroups. Infraspecific variation in indument is relatively common, often parallelling the types of indument

seen on vegetative parts; *D. mandenensis* often has a distinctive flocculent indument. Bracteole scars or persistent bracteoles in most species are located immediately or shortly beneath the flower, but in some species, the upper part of the pedicel elongates during floral expansion so that the scars after anthesis are located well below the flower, sometimes as low as the midpoint of the pedicel. Indument of the upper part of the pedicel then sometimes resembles that of the calyx. Buds are normally broadly obovoid to broadly ellipsoid, with rare exceptions; *D. danguyi* Hochr. is distinguished by near-cylindrical buds with a narrowed apex.

All species of *Dombeya* sect. *Decastemon* have hermaphroditic flowers. Floral characters useful in identification of species include the size of the flowers and the individual floral parts, petal shape, stamen number, sepal and ovary indument, and whether sepals are reflexed after anthesis. Though flower color elsewhere in the genus varies from white to pink or red, all species of *Dombeya* sect. *Decastemon* with reported flower color have white to cream petals (rarely with reddish basal spots), which dry to a dull orange color post-anthesis. Patches of nectariferous trichomes at the bases of the sepals, reported in *Dombeya* by Vogel (2000), are almost always present, though usually small and inconspicuous or concealed by the sepal cup; in a few species, they are consistently large and conspicuous. A few species have suborbicular petals that are spread open at anthesis. A large group of short-peduncled species here included within *Dombeya* ser. *Selinala*, having usually narrow, often lanceolate leaves and a western, dry-habitat distribution, is distinguished by having petals that are usually nearly symmetrical and, at anthesis or at least post-anthesis, somewhat concave apically or throughout. Some members of that series also have staminodes that are shorter than the filaments of the longest fertile stamens, whereas the more common state in *Dombeya* sect. *Decastemon* is for the staminodes to roughly equal or exceed the longest stamens. Stamen number is variable within some species (to the extent of five more or fewer than the baseline value of usually 10 or 15) but seems to be invariant within others. Unequal length of stamens within each group of two or three is typical. *Dombeya gautieri* and two newly described species consistently have five stamens that, unlike the typical condition in *Dombeya*, are oppositisepalous and so short that they are almost hidden by the ovary.

Fruit and seed characters certainly have the potential to aid in identification of *Dombeya* species. Unfortunately, little or no mature fruit has been collected for most species, including most of those for which multiple collections have been made. This dearth of specimens may be because the capsules in this section are usually only a few millimeters in size, and fruiting individuals in the field may appear to collectors to be at a relatively uninteresting post-flowering stage, with the androecium lost but fruit not yet developed, when there is actually near-mature fruit present. Available material shows useful variation in fruit size, shape (usually subglobose, varying to broadly ellipsoid or rarely cylindrical), and indument. Though two ovules per locule in flower is the norm, in most species with fruiting collections only one or two (seldom three) seeds develop per fruit; six seeds may mature, at least sometimes, in two observed species. Seeds vary in size, shape, and color; because of limited material, for some species it is impossible to confirm that apparently small or pale seeds are fully mature. A few species are observed to have an inflated ovary with considerable empty space within when the ovules are small.

Materials and Methods

Herbarium specimens at P and MO were studied, and some species were collected and observed in the field. All measurements were taken from herbarium specimens. For convenience, descriptions do not specify the absence of atypical character states (e.g., inflorescences are umbellate unless stated to be cymose; trichomes, scales, and papillae are pale unless stated to be reddish). For practical reasons, a taxonomic species concept was used whereby three fixed morphological differences were required to recognize populations as distinct species; fewer qualitative differences or overlapping quantitative differences that are geographically correlated were recognized at the subspecific level. Ecological preferences were also taken into consideration. Diagnoses of new species are given in English rather than Latin, as permitted after 1 January 2012, because English is more accessible to the scientific community in Madagascar than is Latin. Preliminary evaluation of conservation status according to IUCN Red Data List criteria (IUCN, 2001) was performed for each taxon recognized herein.

Some aberrant specimens were identified as possible or likely hybrids. Suggestions regarding the parentage of these specimens are based on morphological characters, since no genetic data are available. At least eight or possibly nine species of this section are speculated to be parents of hybrid specimens, with some parents unidentified. A majority of the species that are widespread or frequent enough to be known from more than a handful of collections are implicated in the parentage of at least one hybrid. Given the apparent frequency

of hybridization, certain previously published taxa known only from a single specimen may be suspected to be of hybrid origin; these are discussed below.

Taxonomic Treatment

Dombeya Cav., nom. cons., Diss. 2, Secunda Diss. Bot., App. [1–2]. 1786. TYPE: *Dombeya palmata* Cav. [≡ *Dombeya acutangula* Cav.], designated by Green in Prop. Brit. Bot., 105. 1929.

Assonia Cav., Diss. 2, Secunda Diss. Bot., App. [2]. 1786. TYPE: *Assonia populnea* Cav. [≡ *Dombeya populnea* (Cav.) Baill.].

Cavanilla J. F. Gmel., Syst. Nat. 2: 999, 1037. 1791 [1792]. TYPE: non designatus. Gmelin included all of Cavanilles' (1787) species of *Dombeya* within *Cavanilla*, but since those species were not published with the genus (1786), the name is not illegitimate.

Walcuffa J. F. Gmel., Syst. Nat. 2: 998, 1029. 1791 [1792]. TYPE: *Walcuffa torrida* J. F. Gmel. [≡ *Dombeya torrida* (J. F. Gmel.) Bamps].

Astrapaea Lindl., Coll. Bot. (Lindley), tab. 14. 1821. TYPE: *Astrapaea wallichii* Lindl. [≡ *Dombeya wallichii* (Lindl.) Benth. ex Baill.].

Xeropetalum Delile in Cailliaud, Voy. Méroé 4: 374. 1827. TYPE: *Xeropetalum quinquesetum* Delile [≡ *Dombeya quinqueseta* (Delile) Exell].

Hilsenbergia Bojer, Ann. Sci. Nat., Bot., sér. 2, 18: 189. 1842, nom. illeg., non *Hilsenbergia* Tausch ex Meisn., 1840. TYPE: *Hilsenbergia cannabina* (Hils. & Bojer) Bojer [≡ *Dombeya cannabina* Hils. & Bojer ex Hook.].

Trees or shrubs. Leaves alternate, petiolate, stipulate, simple, highly variable in shape; margin usually ± toothed or palmately (pinnately in *Dombeya gautieri*) lobed, marginal glands frequent in some subgroups; domatia sometimes present. Inflorescences axillary or subterminal, cymose, often umbelliform, or umbellate; multibranched cymes often bracteate; bracteoles 3, free to the base. Flowers hermaphroditic or rarely dioecious; sepals 5, frequently with glandular patches at the base of the adaxial surface; petals 5, white to pink, red or yellowish, persistent; lowermost portion of androecium fused into a corona; staminodes 5; stamens 5 to 45, oppositipetalous or rarely oppositisepalous; ovary superior, 2- or 3(4)-loculed or 5-loculed; style 2- or 3(4)-lobed or 5-lobed, very rarely free to the base. Fruit a loculicidal capsule with 1 to 8 seeds per locule; seeds without wings or arils; cotyledons bifid.

Distribution and habitat. *Dombeya* is native to Madagascar, Africa (extending to the Arabian Peninsula), and the Comoros and Mascarenes. Species are most numerous and morphologically diverse in Madagascar. Habitats are highly variable.

Dombeya sect. **Decastemon** Planch., Fl. Serres Jard. Eur. 6: 225. 1850. TYPE: *Dombeya decanthera* Cav.

Leaves highly variable in shape, usually much longer than broad, usually < 15 cm long; margins usually toothed, seldom sinuate or subentire (in *Dombeya gautieri* pinnately lobed); venation usually ± semicraspedodromous (in 3 species reticulodromous, in *D. gautieri* sometimes fully craspedodromous); marginal glands almost always present; domatia absent or present. Inflorescences umbellate (in 2 species a small, dichotomously branching cyme). Sepals almost always with glandular patches, reflexed or not; petals of small to medium size (to 17 mm); stamens 5 to 15(to 20); ovary 2- or 3(or 4)-loculed. Fruit, where known, with 1 or rarely 2 maturing seeds per locule or 1 per fruit.

Distribution and habitat. *Dombeya* sect. *Decastemon* is endemic to Madagascar, where it is widely distributed and occurs in most vegetation types, ranging from dry forest and bush to humid forest.

Discussion. In the taxonomic treatment presented here, *Dombeya* sect. *Decastemon* includes 41 species, within four of which a total of 11 subspecies are recognized. Preliminary estimates of conservation status suggest that 29 species are threatened at some level (seven Critically Endangered, 11 Endangered, 11 Vulnerable), not counting four probably threatened species that are known from only a single collection but rated Data Deficient because of the inaccessibility of the locality. Nine subspecies are estimated to be threatened at some level (two as Endangered, seven as Vulnerable). Eleven species and two subspecies are known only from the type collection or, in the case of *D. mangorensis* Arènes, the type and a second specimen simultaneously collected. At least four and perhaps as many as six additional species have been collected from only a single population.

Few taxa, therefore, can be described as common. The most widespread and frequently collected species are *Dombeya subviscosa* subsp. *subviscosa* Hochr. in the northwest and *D. lecomtei* Hochr. in the drier parts of the south. The four other species or subspecies whose status was estimated as Least Concern are all southern or western. All of the taxa native to eastern humid forests are rare or narrowly distributed, although several (e.g., *D. mandenensis*, *D. australis* subsp. *grandiflora* Arènes) are locally common within their areas of endemism.

KEY TO THE SERIES OF *DOMBEYA* SECT. *DECASTEMON*

1a. Fertile stamens 5; staminodes oppositipetalous, spreading on top of petals; corona 0.2–0.5 mm, ± spreading, in two species entirely hidden beneath ovary; extreme northern Madagascar ... IV. *Dombeya* ser. *Pentandrae* Appleq.
1b. Fertile stamens (5 to)10 to 15(to 20); staminodes ± oppositisepalous, not spreading; corona variable in length, normally > 0.5 mm, erect, never hidden beneath ovary.
2a. Petals < 10 mm, symmetrical (to slightly asymmetrical), mostly convex at least around apical margin at anthesis (rarely later); leaves lanceolate to ovate (elliptical, oblong-elliptical, oblanceolate); inflorescences umbelliform, with peduncle usually shorter than pedicels, or in *D. parvipetala* dichotomizing cymes; most from dry western, southern, or northern Madagascar, rarely in the east ..... V. *Dombeya* ser. *Selinala*
2b. Petals variable in size and shape, sometimes strongly asymmetrical, not convex; leaves variable in shape, ranging from lanceolate to elliptical, oblong-elliptical, or oblanceolate to obovate; inflorescences umbelliform, with peduncle shorter or longer than pedicels.
3a. Pedicel conically thickened or sharply bent just below flower; peduncle always much shorter than pedicels; dry (to transitional) habitats ..... VI. *Dombeya* ser. *Squamigerae* Arènes
3b. Pedicel not conically thickened or sharply bent below flower; peduncle shorter or longer than pedicels.
4a. Stipule scars broad, usually hemielliptical or irregularly crescent-shaped, on young twigs pale (rarely darker than twig) and usually slightly prominent, or stipules persistent and twigs pilose.
5a. Leaves oblanceolate or narrowly elliptical to oblong-elliptical (obovate, elliptical), never pilose ..... III. *Dombeya* ser. *Mananarenses*
5b. Leaves elliptical to ovate, sometimes broadly so (to narrowly elliptical or narrowly lanceolate), midrib or entire leaf surface normally pilose ..... II. *Dombeya* ser. *Decantherae* (Arènes) Appleq.
4b. Stipule scars narrow, usually linear to very narrowly elliptical, on young twigs usually dark (pale), not prominent (bark below the proximal margin may be elevated); stipules generally caducous, twigs never pilose.
6a. Peduncle usually longer than pedicels; leaves obovate to oblanceolate or narrowly elliptical; southeastern to eastern Madagascar ..... I. *Dombeya* ser. *Apikyenses* Arènes
6b. Peduncle usually mostly shorter than pedicels (in one southwestern species, *D. seyrigiana* Arènes, similar in length or longer); leaves ovate, lanceolate, or elliptical; southeastern to eastern and southwestern Madagascar ..... VI. *Dombeya* ser. *Squamigerae*

I. Dombeya ser. **Apikyenses** Arènes, Candollea 16: 400. 1958. TYPE: *Dombeya apikyensis* Arènes.

Young twigs papillate, scurfy, stellate, or sparsely fimbriate-lepidote; stipule scars on young twigs narrow and usually inconspicuous. Leaves obovate to narrowly elliptical or less often oblanceolate (especially when immature); basal veins 1 to 5; secondary veins 4 to 8(to 10); domatia absent or present; petioles papillate or scaly to stellate or glabrate. Inflorescences umbellate, stellate to minutely papillate and/or scaly; peduncles 7–43 mm, usually longer than pedicels, sometimes in part shorter. Petals broadly obovate to obovate, asymmetrical to near-symmetrical, not convex; stamens 10 to 15; staminodes ± oppositisepalous, longer than longest fertile filaments; ovary stellate to scaly stellate or papillate.

Distribution and habitat. *Dombeya* ser. *Apikyenses* is native to humid forests at elevations from 681 to 1342 m.

Discussion. As herein circumscribed, *Dombeya* ser. *Apikyenses* includes four species with relatively long-peduncled inflorescences compared to many members of the section and small, obovate to narrowly elliptical leaves. Unlike *Dombeya* ser. *Mananarenses*, species of this series have relatively narrow and inconspicuous stipule scars. Material of all species is very limited. The series is not presumed to be monophyletic and is used for the sake of convenience. The placement of *D. ramiovensis* (Arènes) Appleq., which possesses features not otherwise seen in any of the long-peduncled species, is particularly problematic.

KEY TO THE SPECIES OF *DOMBEYA* SER. *APIKYENSES*

1a. Ovary at anthesis papillate, seldom also bearing a few stellate trichomes or scales.
2a. Leaves obovate to narrowly obovate; basal veins 1(to 3, the outer very weak); domatia absent; stamens 10 ..... 1. *D. apikyensis*
2b. Leaves narrowly elliptical to oblanceolate, occasionally to obovate or lanceolate-elliptical; basal veins 3 to 5; small domatia present on some leaves in axils of basal and/or lower secondary veins; stamens 5(to 10) ..... 4. *D. ramiovensis*
1b. Ovary at anthesis stellate or scaly stellate.
3a. Leaves irregularly crenate apically to subentire, with glands variably located; midrib not pilose; inflorescence reddish stellate; Toamasina ..... 2. *D. aquifoliopsis* Hochr.
3b. Leaves serrate at least apically, with glands in tooth apices; midrib of most leaves sparsely pilose; inflorescence pale-colored stellate (to glabrous on peduncle); Fianarantsoa ..... 3. *D. midongyensis* Arènes

1. Dombeya apikyensis Arènes, as "*spikyensis*," Candollea 16: 401. 1958. TYPE: Madagascar. Toliara: bassin de reception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, mont Apiky au–dessus de Mahamavo, transition du bush xérophile à la forêt basse sclerophylle, 800–900 m, Jan.–Feb. 1934 (fl.), *H. Humbert 13798* (holotype, P!; isotype, P [4]!).

Tree to 10 m; twigs grayish brown, the youngest dark or reddish to pale brown, bearing minute papillae and rare small stellate trichomes or scales; stipules caducous, deltoid, 0.5–1.8 mm, dark, bearing few minute papillae; stipule scars on young twigs narrow, not prominent. Leaves obovate to narrowly obovate, 3–6 × 1.2–3.2 cm; petiole 3–9 mm, bearing minute flattened papillae and rare stellate trichomes or scales, often glabrate and wrinkled at maturity; base cuneate; apex rounded to acute or cuspidate with rounded tip; margins crenulate on apical portion to shallowly wavy or subentire, glands inconspicuous, variably located; abaxial surface glabrous or bearing sparse minute whitish to reddish flattened papillae at least on midrib, occasionally sparsely pilose only on midrib; basal veins 1(or 3, the outer very weak); secondary veins 4 to 8 per side, slightly curved, almost craspedodromous, barely visible on adaxial surface; domatia absent. Inflorescences (3- to)5- to 10-flowered; peduncle (1–)2–4.3 cm; pedicels 5–10 mm; peduncle and pedicels bearing minute flattened papillae and sometimes rare small, flat-stellate trichomes; bracteoles caducous, ovate to lanceolate, 0.5–1.3 mm, sparsely papillate, at maturity bracteole scars immediately or slightly beneath flower. Sepals 3.5–5 mm, usually but not always reflexed at anthesis, bearing minute papillae and sometimes scales; petals white, 5–7 × 2–4.4 mm, broadly obovate or obovate, asymmetrical; corona 0.7–0.9 mm; stamens 10; filaments 0.5–1 mm, sometimes partly fused above corona; anthers 0.7–0.8 mm; staminodes linear, 3–3.5 mm; style (0.5–)1–1.3 mm; style branches two, 1.5–1.8 mm, curled or erect; ovary papillate. Fruit unknown.

Distribution, habitat, and phenology. *Dombeya apikyensis* is native to a small region of southeastern Madagascar, where it may occur in humid forest or transitional vegetation or bush at altitudes from 681 to 900 m. It flowers in January and perhaps February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya apikyensis* is noted as Vulnerable or VU, D, with the criterion D referring to very small or restricted populations. The two known collections were made very close together and probably represent a single population; because of its limited area of occupancy, the species is vulnerable to human activities or stochastic events. Since thousands of collections have been made from Andohahela National Park, it is likely that this species is very rare or it would be more often collected.

Discussion. *Dombeya apikyensis* is distinguished by its papillate indument on leaves, inflorescences, and ovaries, and by its very narrow-based leaves that lack domatia. The epithet of *D. apikyensis*, referring to Mt. Apiky, was incorrectly rendered as *spikyensis* in the protologue of Arènes' (1958) publication (p. 401) but as *apikyensis* in the key (p. 274); the journal's volume index listed it as *apikyensis* (p. 455), with a second entry (p. 458) for "*spikyensis*, *errore: apikyensis*." The spelling was corrected in Arènes (1959) and in later databases, as permitted by Article 60.1 of the ICN (McNeill et al., 2012).

Additional specimens examined. MADAGASCAR. **Toliara:** Anosy, Parc National d'Andohahela, parcelle I, *Andriamihajarivo et al. 1098* (MO).

2. Dombeya aquifoliopsis Hochr., Candollea 3: 29. 1926. TYPE: Madagascar. Analamahitro [forêt d'Analamaitso, dans le haut bassin du Bemarivo et de l'Onilahy, Aug. 1907], bois secs, 800 m, s.d. (fl.), *H. Perrier de la Bâthie 5617* [*H. L. Jumelle 40*] (holotype, G not seen, G image!; isotypes, K not seen, K image!, P!).

Dombeya andilamenensis Arènes, Candollea 16: 397. 1958, syn. nov. TYPE: Madagascar. Toamasina: forêt de l'Anona près Andilamena, distr. d'Ambatondrazaka, 900 m, June 1938 (fl.), *G. Cours 271* (holotype, P!).

Understory shrub to 5 m; twigs grayish brown, the youngest with an indument of small irregular scales, somewhat stellate to papillose; stipules caducous, not seen; stipule scars on young twigs narrow, not prominent. Leaves obovate, or when immature narrowly elliptical to oblanceolate, 3–5.2 × 1.6–3.4 cm, coriaceous; petiole 2–5.5 mm, scaly stellate; base cuneate, rounded at the extreme base; apex cuspidate to short-acuminate or acute with a rounded tip; margins irregularly crenate apically to subentire especially in young leaves, with inconspicuous glands variably located in convex or concave portions; both surfaces sparsely stellate, mostly along main veins, or glabrous at maturity; basal veins 3(to 5), the lateral weak; main secondary veins above the base 4 to 7 per side, with weaker similar veins often interspersed, venation visible on adaxial surface, fairly prominent

on adaxial surface; domatia absent. Inflorescences (1)2- to 4(5)-flowered, sometimes bracteate probably as an aberration; peduncle, where present, 1.1–2.2 cm; pedicels (2–)8–12 mm; peduncle and pedicels reddish stellate; bracteoles caducous, ovate, 1.5–3.5 mm, stellate, bracteole scars at maturity slightly beneath flower. Sepals 4.5–5 mm, usually reflexed in late anthesis, reddish stellate to scaly stellate, glandular patches sometimes absent; petals white, (5.8–)6.8–8.5 × 5–6 mm, broadly obovate, asymmetrical; corona 1 mm; stamens 10 to 15; filaments white, 0.5–1.5 mm; anthers 0.7–1.2 mm; staminodes white, linear, 2–3.5 mm; style white, 3–5 mm, stellate basally; style branches two or three, 1.5–2 mm, irregularly curled; ovary stellate or scaly stellate. Old fruit broadly ovoid, 5.4 × 3 mm, pale, with persistent indument.

Distribution, habitat, and phenology. *Dombeya aquifoliopsis* has been collected in humid forests of eastern Madagascar at 800–900 m. It appears to be winter-flowering, with the only known flowering date in June.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya aquifoliopsis* is noted as Endangered or EN B1ab(iii)+2ab(iii). The B criterion generally refers to the geographic range as expressed by B1, extent of occurrence (EOO), or B2, area of occupancy. Only two older collections are known, and degradation of potential habitat continues in these areas.

Discussion. *Dombeya andilamenensis* was supposedly characterized by a stellate-pubescent ovary, in contrast to the scaly ovary of *D. aquifoliopsis*; the observed induments in fact reflect the possible range of morphologies for a species with rather flat-stellate or long-fimbriate scales, as is seen in several more frequently collected species (most notably *D. lucida* Baill. in *Dombeya* sect. *Xeropetalum*; Applequist, pers. obs.). The type of *D. andilamenensis* has smaller inflorescences but is barely flowering, with most inflorescences still in bud; sepal glands are lacking or nearly lacking in the type of *D. aquifoliopsis*. The two are otherwise generally similar in morphology, and the names are, therefore, synonymized.

Arènes (1958) lectotypified several of Hochreutiner's (1926) names using the P duplicate of the single collection or one of the syntypes cited by Hochreutiner. However, for *D. aquifoliopsis* Hochreutiner's publication provided internal evidence that the duplicate of the single cited specimen conserved at G (where he was then working) was the intended type. Hochreutiner (1926: 29) quotes only the label data from the G duplicate of the type: "Analamahitro, bois secs, alt. 800 m., (Herb. Perrier de la B., n. 40 de Jumelle)." The P and K duplicates, which additionally number the collection as *Perrier de la Bâthie 5617*, have different label text, as noted above, which was not quoted by Hochreutiner. Further, many of the specimens Hochreutiner cited, including Perrier specimens, have designations such as "in Hb. Paris" or "in Hb. Kew et Paris," permitting the assumption that specimens lacking such designations were located at G. Since the specimen at G was the only original material seen by Hochreutiner, it is appropriately treated as a holotype, and Arènes' lectotypification can be rejected as unnecessary.

3. Dombeya midongyensis Arènes, Candollea 16: 396. 1958. TYPE: Madagascar. Fianarantsoa: Midongy du Sud, prov. Farafangana, 23 Aug. 1926 (fl.), *R. Decary 5142* (holotype, P!; isotype, P!).

Small tree or large shrub; twigs dark brown, sparsely stellate with short trichomes; stipules sometimes persistent, narrowly lanceolate to linear, (2.5–)3.5–7 mm, stellate; stipule scars on young twigs narrow, not prominent. Leaves obovate, 3.5–6 × 1.6–3.1 cm; petiole 4–11 mm, short-stellate; base cuneate, sometimes rounded at extreme base; apex cuspidate to irregularly rounded; margins serrate at least on distal half with brownish glands in tooth apices; adaxial leaf surface sparsely stellate along main veins, often glabrate at maturity; abaxial surface sparsely stellate, often sparsely pilose on midrib; basal veins 3, the lateral weak; secondary veins 5 to 8 per side, inconspicuously visible on adaxial surface; domatia absent. Inflorescences (1)2- or 3(4)-flowered, occasionally a 3-branched bracteate cyme; peduncle 2–4.3 cm, glabrous or sparsely stellate; pedicels 8–11 mm (to 20 in solitary flowers), stellate; bracteoles caducous, lanceolate to linear, (1.5–)2.5–3.5 mm, stellate, borne immediately beneath flower. Sepals 5–6 mm, not reflexed at anthesis (some possibly becoming reflexed later), stellate; petals white, 6–8.5 × 4–6 mm, broadly obovate, nearly symmetrical; corona 1 mm; stamens ca. 15; filaments 0.6–2 mm; anthers 1–1.3 mm; staminodes narrowly spatulate, 4–5 mm; style 1.8–2.4 mm, stellate at base; style branches two, 1(–2) mm; ovary stellate.

Distribution, habitat, and phenology. The only known collection of *Dombeya midongyensis* is from humid forest in southeastern Madagascar; it was in flower in August.

IUCN Red List category. As a distinct species, the preliminary IUCN Red List category (IUCN, 2001) for *Dombeya midongyensis* is Critically Endangered or CR, D. Only one locality is known; it is not known whether the type collection (from 1926) was made in what is now the protected area of Midongy du Sud. Unsuccessful efforts were made by the author to relocate the species in several forests around Midongy du Sud and Befotaka during the apparent flowering season (August) with the assistance of an experienced local ranger. It is, therefore, possible to conclude that if this taxon is still present at all, it is very rare and fewer than 50 mature individuals are likely to exist.

Discussion. It may not be certain that *Dombeya midongyensis* is a distinct species. *Dombeya midongyensis* is known from a single specimen whose indument includes sparse stellate pubescence on the twigs, petioles, and leaves as well as pilose indument on the midribs of most leaves. The lack of additional specimens with similar morphology provides cause for suspicion that the type of *D. midongyensis* might be a hybrid involving *D. decanthera* subsp. *farafanganica*, the only other species with pilose indument confined to the midribs, and some small-leaved species having narrow stipule scars and leaves broadest above the midpoint. The former taxon has been collected from Befotaka, which is in the vicinity of Midongy du Sud. The dual indument on the leaves might also suggest hybridization, though two species of *Dombeya* subg. *Dombeya* from the Mascarenes that are known from multiple collections are reported to have a mixed stellate and sparsely pilose indument (Friedmann, 1987).

4. Dombeya ramiovensis (Arènes) Appleq., comb. et stat. nov. Basionym: *Dombeya farafanganica* Arènes subsp. *ramiovensis* Arènes, Candollea 16: 403. 1958. TYPE: Madagascar. Fianarantsoa: Ramiova, RN V [Andringitra], canton Sendrisoa, distr. Ambalavao, 6 June 1951 (fr.), *Reserves Naturelles 3069* (holotype, P!; isotype, P!).

Shrub or tree to 6 m; twigs grayish to dark grayish brown, the youngest ± fimbriate-lepidote, often reddish, or sparsely papillate, with leaf scars very prominent; stipules caducous, lanceolate to deltoid, 1–4.5 mm, with flat scurfy to fimbriate-scaly indument; stipule scars on young twigs narrow, not prominent. Leaves narrowly elliptical to oblanceolate, sometimes tending toward obovate or lanceolate-elliptical, 3–12 × 1–4.1 cm; petiole 2.5–13 mm, fimbriate-lepidote (often reddish) to glabrate or papillate; base cuneate to rounded; apex acute to short-acuminate with a usually rounded tip or rounded to shallowly emarginate; margins crenulate, especially apically, to subentire, with marginal glands variably located, usually inconspicuous, occasionally projecting slightly; adaxial surface glabrous; abaxial surface glabrous to glabrate with few stellate trichomes, especially when young, or bearing minute reddish papillae; basal veins 3 to 5, the outer weak; secondary veins above the base 4 to 8(to 10) per side, occasionally with subscalariform tertiary venation, visible but inconspicuous on upper surface; domatia present, small with few straight trichomes, basal and/or in axils of lower secondary veins. Inflorescences (1)2- to 7-flowered; peduncle 0.3–2.8 cm, rarely paired in axils; pedicels (1.5–)4–10 mm, shorter or longer than peduncle; peduncle and pedicels fimbriate-lepidote to substellate, sometimes densely so on peduncle and often reddish, or sparsely papillate; bracteoles sometimes persisting beyond anthesis, linear to lanceolate or narrowly deltoid, 0.5–2.5 mm, scaly to glabrous, borne immediately beneath flower. Sepals 2.5–4.4 mm, often reflexed after anthesis, minutely papillate, sometimes with sparse flattened stellate trichomes or scales, to glabrate, or with sparse to moderate scurfy indument; petals 4–5.8 × 1.7–3.1 mm, obovate, asymmetrical; corona 0.4–1.5 mm; stamens 5(to 10); filaments 0.5–1.5 mm, sometimes partly fused above corona; anthers 0.5–1 mm; staminodes linear, 1.5–3.4 mm; style 1–2.4 mm, sometimes deeply divided, glabrous; style branches two, 1–2(–3) mm, sometimes papillate, curled; ovary papillate, occasionally in part sparsely fimbriate-lepidote. Immature fruit subglobose often with remains of style base at apex, to at least 2 mm diam., sometimes shallowly ridged, pale brown, papillate, with style and stigma branches persisting; developing ovules possibly 2, with empty space in ovary before seeds mature.

Distribution, habitat, and phenology. *Dombeya ramiovensis* is native to southeastern Madagascar; it has been reported to occur on marble substrate up to 1342 m. The species flowers in March and April, and immature fruits have been collected in June and September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ramiovensis* is noted as Vulnerable or VU, D. Two historical locations are known, so the area of occupancy is likely to be small. One of those localities is unprotected and subject to continued habitat loss, and the species' persistence at the other has not been confirmed by recent collection.

Discussion. Placement of *Dombeya ramiovensis* is difficult. Although this treatment maintains its traditional placement with other long-peduncled southeastern species, several characters suggest a possible relationship to the three very distinctive species of *Dombeya* ser. *Pentandrae*: leaves with domatia in axils of secondary veins, stamens frequently only five, style sometimes deeply divided, and inflated fruits with empty space inside at an early stage of development. Although each of these characters is rare, none is entirely unknown elsewhere in *Dombeya* subg. *Xeropetalum*, and the flowers, with narrow, erect, oppositisepalous staminodes and well-developed corona and filaments, show none of the other derived characteristics of *Dombeya* ser. *Pentandrae*. Domatia bear small clusters of unbranched trichomes, while those of *Dombeya* ser. *Pentandrae* do not. It is, however, possible that this species represents the sister group of that series.

Arènes (1958, 1959) treated *Dombeya ramiovensis*, then known only from the type, as a subspecies of *D. farafanganica*, but it has significant differences from that taxon (herein recognized at the subspecific level within a more broadly circumscribed *D. decanthera*), which has broader, longer-petioled leaves with no domatia, usually pilose midribs and often conspicuous papillae, and broadened prominent stipule scars. The inflorescences and flowers of *D. decanthera* are also somewhat larger. *Dombeya ramiovensis* is much more likely to have close affinities to *D. apikyensis*, another small-flowered southeastern species that shares the probably derived character of narrow stipule scars; that species lacks domatia and has more usually obovate leaves with one basal vein.

Four additional specimens herein included in *Dombeya ramiovensis*, all from Ambatofinandrahana, have much smaller leaves than the type, much smaller stipules, and somewhat smaller inflorescences. The indument is also rather different (inflorescences more or less fimbriate-lepidote vs. sparsely papillate in the type; sepals papillate and often sparsely lepidote to stellate vs. minutely scaly in the type), and stamen number is usually reduced to five rather than 10 as in the type. Since these specimens are from the same region and share the presence of domatia, a rare character in the long-peduncled species, while all of the variable characters enumerated are also seen to vary within certain better collected species, it appears most conservative to treat them all as conspecific. Additional material from Andringitra would be needed to determine definitively whether the two populations should be treated as distinct. One of the collections from Ambatofinandrahana (*Birkinshaw 1318*) has small, probably immature leaves with unusually narrow bases and very few domatia; the ovary sometimes bears a few large apical stellate-lepidote trichomes, a character not seen in any other specimen.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** 8 km S of Ambatofinandrahana, *Birkinshaw 1318* (MO); Ambatofinandrahana, *Bosser 9834* (P); Ambatofinandrahana, "route de Fenoarivo," *Bosser 9836* (MO); "environs d'Ambatofinandrahana ± 10 km route de Fenoarivo," *Descoings 3239* (MO).

II. Dombeya ser. **Decantherae** (Arènes) Appleq., stat. nov. Basionym: *Dombeya* subsect. *Decantherae* Arènes, Candollea 16: 390. 1958. TYPE: *Dombeya decanthera* Cav.

Dombeya subser. *Lavasoenses* Arènes, Candollea 16: 395. 1958. TYPE: *Dombeya lavasoensis* Arènes.

Young twigs papillate, scurfy to flat-stellate, or pilose; stipule scars relatively broad, usually pale, seldom dark, often prominent, or stipules persistent. Leaves elliptical, broadly elliptical, or ovate (seldom to broadly ovate, narrowly elliptical, or lanceolate) or narrowly lanceolate; basal veins 3 to 5; secondary veins 4 to numerous; domatia absent; petioles pilose, papillate, short-pubescent, scaly stellate, or glabrous. Inflorescences umbellate, small dichotomizing cymes, or 1-flowered, papillate or scurfy to flat-stellate (seldom glabrate) or pilose; peduncles absent or (8–)12–49(–54) mm, usually but not always longer than pedicels. Petals broadly obovate to obovate, strongly or less often moderately asymmetrical, not convex; stamens 10 to 15; staminodes ± oppositisepalous, longer than longest fertile filaments; ovary papillate, flat-stellate, or stellate.

Distribution and habitat. *Dombeya* ser. *Decantherae* is native to southeastern Madagascar and has been reported from habitats that include littoral, humid, and transitional forests at low to moderate altitudes (21–500 m, perhaps rarely to 1000 m).

Discussion. The species included within *Dombeya* ser. *Decantherae* might be related to those of *Dombeya* ser. *Mananarenses*. In two species, *D. decanthera* and *D. lavasoensis*, persistent remnants of the stipule bases are often present, giving stipule scars a broad, raised, pale appearance as is typical of the latter series, though a portion of *D. decanthera* has stipule scars that are elevated by outgrowth of the twig beneath them. Both species have generally elliptical to ovate leaves and unusual pilose indument, on the midrib in *D. decanthera* and throughout in *D. lavasoensis*. *Dombeya lavasoensis* has solitary flowers so cannot be placed into a section by

inflorescence morphology, but (with caveats, noted below) it seems better placed in *Dombeya* sect. *Decastemon* than *Dombeya* sect. *Xeropetalum*. The newly described *D. pilosissma* has small few-flowered dichotomizing cymes; like *D. lavasoensis*, it has long-pilose indument on most organs. This is a very unusual character in *Dombeya*. All three of these species are native to southeastern Madagascar, so it seems probable that they form a natural group.

KEY TO THE SPECIES OF *DOMBEYA* SER. *DECANTHERAE*

1a. Leaves normally pilose on midrib, very rarely glabrous, papillate to glabrous or sparsely stellate on rest of surface; inflorescences umbellate (rarely partly cymose), usually long-peduncled ..... 5. *D. decanthera*

1b. Leaves pilose throughout; inflorescences small dichotomizing cymes or flowers solitary.

2a. Leaves narrowly lanceolate, < 10 cm; flowers solitary; petals < 8 mm, obovate and moderately asymmetrical ... 7. *D. pilosissima*

2b. Leaves ovate to elliptical, < 10 cm; flowers borne at least partly in small cymes; petals > 8 mm, broadly obovate and strongly asymmetrical ..... 6. *D. lavasoensis*

5. Dombeya decanthera Cav., Diss. 3, Tertia Diss. Bot., 126, tab. 40, fig. 2. 1787. *Melhania decanthera* (Cav.) DC., Prodr. [A. P. de Candolle] 1: 499. 1825. TYPE: Madagascar, s.d. (fl.), [*P.*] *Commerson s.n.* (lectotype, designated by Arènes [1958: 406], P!; isolectotypes, C not seen, C image!, MA not seen, MA image!, MPU [2] not seen, MPU [2] images!).

Tree or rarely a large shrub; twigs brown to grayish, the youngest bearing papillae, sometimes reddish and/or scurfy scales, with occasional flat-stellate trichomes; stipules caducous or seldom persistent, lanceolate to deltoid, sometimes acuminate, 0.6–5.5(–12) mm, sparsely scaly, occasionally also stellate; stipule scars frequently prominent, pale or dark, crescent-shaped to hemielliptical. Leaves broadly elliptical to elliptical, ovate, or broadly ovate, less often narrowly elliptical to lanceolate, 4.5–14(–16.5) × (2–)2.5–6.5(–7.5) cm; petiole (0.6–)1.8–3.4(–3.8) cm, glabrous, papillate, pubescent with short straight trichomes, or scaly, seldom with few stellate trichomes; base broadly cuneate to cuneate or rounded or rarely attenuate; apex acuminate to cuspidate or long-apiculate, occasionally acute, rounded, or emarginate; margins shallowly wavy to crenate or crenate-dentate, seldom subentire or with few serrate teeth apically, with marginal glands inconspicuous, sometimes absent, located in marginal concavities or near tooth apices; adaxial surface glabrous or papillate; abaxial surface normally pilose on midrib, very rarely glabrous, elsewhere inconspicuously flat-papillate, sometimes with reddish papillae, or glabrous, occasionally with few small stellate trichomes; basal veins (3 to)5, if 5 the outer weak; secondary veins above the base 4 to 9(to 11) per side, visible but inconspicuous on adaxial surface; domatia absent. Inflorescences 3- to 15(to 21)-flowered; peduncle (0.8–)1.4–4.9(–5.4) cm or rarely absent or once-branched as an aberration, normally but not always longer than pedicels; pedicels (4–)5.5–18(–21) mm; peduncle and pedicels papillate, sometimes with dark or reddish papillae, and/or with a sparse indument of small scurfy to flat-stellate scales, less often glabrate; bracteoles sometimes persisting beyond anthesis, 0.6–3.1 mm, varying from linear, narrowly oblong, lanceolate, or spatulate to ovate or broadly elliptical, papillate and/or scaly, borne immediately beneath flower. Sepals (2.8–)3.5–6(–6.8) mm, usually reflexed after anthesis, with indument of small or flat-stellate trichomes or scales and sometimes papillae; petals white, (4.9–)6–9.5 × (2.8–)3.2–6.5(–7) mm, obovate to broadly obovate, usually strongly asymmetrical especially when relatively narrow; corona 0.7–1.8 mm, narrowed above ovary; stamens 10(to 15); filaments 0.5–1.6(–2.5) mm, sometimes partly fused above corona; anthers orange to yellow, 0.5–1(–1.3) mm; staminodes linear, 2.3–5(–5.5) mm; style (0.8–)1.5–3.5(–4) mm, rarely deeply divided, the basal portion papillate and/or pubescent or stellate, or rarely glabrous; style branches 2(3), (0.8–)1.5–3 mm, papillate or bearing indument like that of style, usually curled; ovary papillate, sometimes with a few larger semi-stellate scales or apical stellate trichomes. Fruit (known only from *Dombeya decanthera* subsp. *farafanganica* (Arènes) Appleq.) broadly elliptical, to 3 mm high, 2.4 mm diam., with persistent style base, pale, papillate; only 1 seed per fruit maturing, broadly ellipsoid, 2.5 mm, pale brown with minutely textured surface, 2 distinct grooves on one side.

Discussion. *Dombeya farafanganica* is herein treated as two subspecies of *D. decanthera*, as both encompass enough morphological variability that it is not possible to define a suite of fixed characters that separate them at the species level. While *D. decanthera* is widespread and found in a variety of habitats, the three subspecies recognized have more limited ecological ranges.

Several sheets of *Dombeya decanthera* collected by Commerson exist; none have dates or locality data. Though the P specimen is somewhat atypical of the group of populations around the city of Tôlanaro (Fort Dauphin) herein treated as *D. decanthera* subsp.

decanthera, that does seem on morphological grounds to be its most likely affinity. Two sheets held by MPU, which have not been seen by this author but whose images are available on JSTOR (<www.jstor.org>), have been presumed to be type material. The larger and more mature of these has more strongly toothed margins than the specimen at P, so bears a stronger resemblance to *D. decanthera* subsp. *latifolia* (Arènes) Appleq., though its stipules are short. The slightly different appearance may indicate that the MPU specimens are of a different individual, potentially collected at a different time or place than the P specimen; however, intraindividual variation can be significant.

KEY TO THE SUBSPECIES OF *DOMBEYA DECANTHERA*

1a. Leaf margins usually crenate-dentate with prominent teeth, glands variably placed but usually near tooth apices; inflorescences 3- to 5(to 9)-flowered; littoral forests along southeastern coast ..... 5c. subsp. *latipetala* (Arènes) Appleq.

1b. Leaf margins shallowly wavy to crenate or crenate-dentate, glands variably placed, often located between teeth; inflorescences (3- to)5- to 15(to 21)-flowered; humid and transitional forests.

2a. Leaves variable in shape, 4.5–9.5(–12) × 1.7–5(–5.9) cm; petiole 0.6–2.3(–3.2) cm, papillate or scaly, sometimes sparsely stellate or pilose near leaf base; style (0.8–)1.5–2.5 mm, the lower half usually bearing straight and/or stellate trichomes, rarely papillate or glabrous; extreme southeastern Madagascar ..... 5a. subsp. *decanthera*

2b. Leaves broadly elliptical to elliptical, (7–)8–14(–16.5) × (3.4–)4–6.5(–7.5) cm; petiole (1.5–)1.8–3.4(–3.8) cm, glabrous or pubescent; style (2.2–)2.5–3.5 mm, the basal portion papillate sometimes with a few short trichomes or flattened-stellate scales; eastern Madagascar ..... 5b. subsp. *farafanganica*

5a. **Dombeya decanthera** Cav. subsp. **decanthera**

Dombeya decanthera subsp. *decanthera* var. *bojeriana* (Baill.) Arènes, Candollea 16: 406. 1958, syn. nov. Basionym: *Dombeya bojeriana* Baill., Bull. Mens. Soc. Linn. Paris 1: 495. 1885. TYPE: Madagascar, s.d. (fl.), [*W.*] *Bojer s.n.* (holotype, P!).

Dombeya decanthera subsp. *meridionalis* Arènes, Candollea 16: 406. 1958, syn. nov. TYPE: Madagascar. Toliara: mont Ankazovandamena, près de la baie des Galions (Ranofotsy) au SW de Fort Dauphin, forêt ombrophile sur gneiss, rochers du sommet, 100–450 m, 21 Feb. 1955 (fl.), *H. Humbert & R. Capuron 29082* (holotype, P!; isotype, P!).

Tree to 10 m, 10 cm diam., or shrub to 5 m; young twigs bearing small white or reddish flat papillae or scurfy scales and occasionally a few flat-stellate trichomes; stipules caducous or persistent, lanceolate to deltoid and sometimes acuminate, 0.6–1.5(–2.5) mm, sparsely scaly and stellate; stipule scars on young twigs moderately prominent or not, pale, irregular, hemielliptical but small. Leaves broadly elliptical to broadly ovate, ovate, narrowly elliptical, or lanceolate, 4.5–9.5(–12) × 1.7–5(–5.9) cm; petiole 0.6–2.3(–3) cm, papillate or scaly, sometimes sparsely stellate or pilose near leaf base; base rounded to broadly cuneate, rarely attenuate; apex short-acuminate to long-acuminate, cuspidate, acute with a rounded tip, or rounded; margins shallowly wavy to crenate or crenate-dentate, with glands variably located, sometimes projecting slightly; adaxial surface papillate to glabrous, abaxial surface pilose only along midrib, at least basally, or very rarely glabrous, elsewhere papillate to glabrous, rarely with few small stellate trichomes; secondary veins above the base 4 to 7 per side. Inflorescences (3- to)5- to 15(to 21)-flowered; pedicels 5.5–14 mm; peduncle and pedicels papillate and often bearing a few flat-stellate trichomes; bracteoles sparsely papillate and often scaly stellate. Sepals (2.8–)3.5–5(–5.5) mm, almost always reflexed, with indument of papillae and small flat-stellate trichomes or scales; petals (4.9–)6–8(–9) × (2.8–)3.2–6 mm; corona 0.7–1.1 mm, occasionally narrowed above ovary; anthers 0.5–0.9 mm; style (0.8–)1.5–2.5 mm, occasionally deeply divided, at least the lower half usually short-pilose and/or stellate, rarely papillate or glabrous; style branches (0.8–)1.7–2.5 mm, papillate or sometimes bearing indument similar to that of style; ovary papillate and sometimes bearing stellate trichomes on apical portion. Fruit unknown.

Distribution, habitat, and phenology. *Dombeya decanthera* subsp. *decanthera* is native only to a small region around Tôlanaro (Fort Dauphin) and Andohahela National Park in extreme southeastern Madagascar. It is reported from humid and transitional forests, on thin soil and gneiss, at elevations from 25 to at least 500 m (and perhaps occasionally to 1000 m). Flowering specimens have been collected from December through July; immature fruits have been collected in December.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya decanthera* subsp. *decanthera* is noted as Vulnerable or VU, D. Though it occurs in part on protected land, probably only five distinct populations are known, all in a small geographic area so that either natural events or human activity might affect all populations simultaneously.

Vernacular names. Hafopotsy (*Rabenantoandro et al. 112*), mandoavato (*Randriamampionona 835*),

sely (*Reserves Naturelles 13055*), tanafotsy [?] (*Service Forestier 26053*).

Discussion. Though *Dombeya decanthera* subsp. *decanthera* has a limited geographic range, considerable morphological variation can be observed. Included is one aberrant collection, *Randriamampionona 835*, most of the duplicates of which are near-glabrous and lack the midrib trichomes that normally make this species easy to recognize. Also notably, *Service Forestier 28576* has small obovate to elliptical leaves with three basal veins, which at first glance resemble those of *D. apikyensis* and similar species, small and only slightly broadened stipule scars, and small flowers. However, the leaves sometimes have a few long straight trichomes at the base of the midrib; the bracteoles are small and sometimes persistent; the corona often narrows at the top of the ovary then reflexes outward; and the style bears sparse short white trichomes, while the ovary is papillate. This specimen is suggested to be a hybrid involving *D. decanthera* subsp. *decanthera*, which could contribute all four of those unusual characters, and a smaller-leaved species such as *D. apikyensis*, *D. australis*, or *D. ranofotsyensis* Arènes, the last of which is known from Ranopiso.

Additional specimens examined. MADAGASCAR. **Toliara:** Mihana, Fort Dauphin, *Birkinshaw et al. 449* (P); Mandena, Fort Dauphin, s.d., *M. G. Johnson s.n.* (P); Ambatorongorongo, Amboavola, Fort Dauphin, *Rabenantoandro et al. 112* (P); Andohahela, parcelle 1, *Randriamampionona 420* (MO, P); Andohahela, parcelle 1, *Randriamampionona 433* (MO, P); Andohahela, parcelle 1, *Randriamampionona 835* (MO); Anosy, [Ambatorongorongo], *Razakamalala et al. 4271* (MO); Andohahela, parcelle 1, *Reserves Naturelles 9440* (P); Fort Dauphin, *Reserves Naturelles 13055* (P); Andohahela, *Service Forestier 26053* (P).

Probable hybrid specimen. MADAGASCAR. **Toliara:** Vohitsiandriana, *Service Forestier 28576* (P [4]).

5b. Dombeya decanthera Cav. subsp. **farafanganica** (Arènes) Appleq., comb. nov. Basionym: *Dombeya farafanganica* Arènes subsp. *farafanganica*, Candollea 16: 401–402. 1958. TYPE: Madagascar. Fianarantsoa: Befotaka, province de Farafangana, 12 Aug. 1926 (fl.), *R. Decary 4784* (holotype, P!; isotype, P!).

Dombeya farafanganica [subsp. *endrina* Arènes var. *endrina*] subvar. *endrina*, Candollea 16: 403–404. 1958, syn. nov. TYPE: Madagascar. Toamasina: RN I, canton Ambodiriana, distr. Tamatave, 23 July 1953, *Reserves Naturelles 5920* (holotype, P!; isotypes, P!, TEF not seen, TEF image!).

Dombeya farafanganica [subsp. *endrina*] var. *linearis* Arènes, Candollea 16: 404. 1958, syn. nov. TYPE: Madagascar. Fianarantsoa: Befotaka, prov. de Farafangana, 11 Aug. 1926 (fl.), *R. Decary 4729* (holotype, P!; isotypes, P!, PRE not seen, PRE image!).

Dombeya farafanganica [subsp. *farafanganica*] var. *manakensis* Arènes, Candollea 16: 403. 1958, syn. nov. TYPE: Madagascar. Toamasina: RN 3, canton Manaka Est, distr. Ambatondrazaka, bas fond, 4 Sep. 1951 (fl.), *Reserves Naturelles 3145* (holotype, P!; isotypes, P!, TAN not seen, TAN image!).

Dombeya manaharica Baill., Bull. Mens. Soc. Linn. Paris 1: 491–492. 1885, syn. nov. TYPE: Madagascar. Toamasina: Manahar, s.d. (fl.), [*J.-H. L.*] *Humblot 244* (holotype, P!; isotypes, G not seen, G image!, K not seen, K image!, P [2]!).

Tree to 30 m; young twigs bearing scurfy scales; stipules caducous, lanceolate, often long-acuminate, 4–5 mm, sparsely scaly; stipule scars on young twigs prominent or not, pale or seldom dark, crescent-shaped to hemielliptical. Leaves broadly elliptical to elliptical, (7–)8–14(–16.5) × (3.4–)4–6.5(–7.5) cm; petiole (1.5–)1.8–3.4(–3.8) cm, glabrous or pubescent; base broadly cuneate to rounded; apex short-acuminate to cuspidate or long-apiculate, or rarely in individual leaves rounded or emarginate; margins shallowly wavy to crenate with few long shallow rounded teeth or subentire especially when young, occasionally with few serrate teeth apically, with glands inconspicuous or lacking, often located in marginal concavities; adaxial surface glabrous; abaxial surface pilose only along midrib, elsewhere usually inconspicuously flat-papillate; secondary veins above the base 6 to 8 per side. Inflorescences (5)6- to 15-flowered; pedicels (4–)7–14.5 mm; peduncle and pedicels with a sparse indument of small scurfy to flat-stellate scales and/or papillae or glabrate; bracteoles scaly. Sepals (3.5–)4–5.5 mm, usually but not consistently reflexed, with indument of small stellate trichomes or scales; petals 7–8.6(–9) × (3–)3.5–5.5(–7) mm; corona 1.2–1.8 mm, not narrowed above ovary; anthers (0.5–)0.8–1 mm; style (2.2–)2.5–3.5 mm, the lower portion papillate sometimes with a few short straight trichomes or flattened-stellate scales; style branches (1.5–)2–3 mm, papillate; ovary white post-anthesis, papillate, sometimes with a few larger semi-stellate scales. Fruit broadly elliptical, to 3 mm high, 2.4 mm diam., with persistent style base, pale, papillate; 1 seed per fruit maturing, broadly ellipsoid, ca. 2.5 mm, pale brown with minutely textured surface, 2 distinct grooves on one side.

Distribution, habitat, and phenology. *Dombeya decanthera* subsp. *farafanganica* is found in humid forests of eastern Madagascar at recorded elevations of 250–500 m. It flowers from July to September; mature fruit has been collected in September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya decanthera* subsp. *farafanganica* is noted as Vulnerable or VU B2ab(iii) due to the small number of populations and ongoing destruction of habitat, although it does occur in two protected areas.

Vernacular names. Hafobalo (*Reserves Naturelles 9180*, *Service Forestier 18110*), hafotra (*Reserves Naturelles 3145*), hafotra endrina (*Reserves Naturelles 5920*).

Discussion. *Dombeya decanthera* subsp. *farafanganica* is differentiated from *D. decanthera* subsp. *decanthera* primarily by its larger leaves (to 14[–16.5] cm vs. 9.5[–12] cm) and a different indument, especially on the petiole and style; the corona is never narrowed above the ovary. It has a broader and more northern distributional range. Unfortunately, despite the name, this subspecies does not occur in the vicinity of Farafangana, being found farther inland and at higher altitudes (up to 500 m); collections made near Farafangana are of *D. decanthera* subsp. *latipetala*.

Dombeya farafanganica was described at the species level by Arènes (1958, 1959), who further segregated one specimen as *D. manaharica* because its ovary and style were stellate rather than papillate. The ovaries of the type specimen of *D. manaharica* are largely papillate with limited coverage by flattened stellate trichomes, although one flower in the fragment packet does have relatively dense stellate trichomes. Most styles bear flattened stellate trichomes, and small unbranched trichomes, more densely than is typical of *D. decanthera* subsp. *farafanganica*. This represents, however, an extreme version of the variation in indument already seen in *D. decanthera* subsp. *farafanganica* rather than an entirely novel condition, and the collection is otherwise representative. Most varieties and subvarieties recognized by Arènes are based on highly variable characters and are not useful.

The bark is stated to have presumably useful fiber (*Reserves Naturelles 3145*).

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** Befotaka, Farafangana, *Decary 4729* (P [2]). **Toamasina:** Ambatondrazaka, Bemoasa, *Rakotonandrasana et al. 542* (P); Zahamena, NW of Andratanantsoitra, *Randrianjanaka & Zafy 169* (P); Vohimangitra, canton Ambodiriana, *Reserves Naturelles 9180* (P); Réserve Naturelle Betampona, Ambodiriana, *Service Forestier 18110* (MO, P [2]).

5c. Dombeya decanthera Cav. subsp. **latipetala** (Arènes) Appleq., comb. et stat. nov. Basionym: *Dombeya farafanganica* Arènes [subsp. *endrina* var. *endrina*] subvar. *latipetala* Arènes, Candollea 16: 404. 1958. TYPE: Madagascar. Fianarantsoa: Boma (distr. de Farafangana), 13 Sep. 1954 (fl.), *Service Forestier 12391* (holotype, P!; isotypes, P!, TEF not seen, TEF image!).

Tree to 15 m, 0.5 m diam.; young twigs bearing papillae and usually scurfy scales; stipules caducous or rarely persistent, lanceolate, sometimes long-acuminate, (2.5–)3.5–5.5(–12) mm, sparsely scaly; stipule scars often strongly prominent, pale, irregularly crescent-shaped to hemielliptical. Leaves elliptical to ovate or broadly elliptical, (7–)8–14(–16.5) × (3.2–)4–7(–9) cm; petiole (0.7–)1.4–3(–3.7) cm, usually papillate, sometimes pubescent; base rounded or occasionally cuneate; apex short-acuminate to cuspidate or long-apiculate; margins crenate-dentate, with teeth usually prominent and well defined, with glands inconspicuous but usually present, usually near teeth apices; adaxial surface glabrous; abaxial surface pilose only along midrib, elsewhere flat-papillate with sometimes reddish papillae; secondary veins above the base (4 to)6 to 9(to 11) per side. Inflorescences 3- to 5(to 9)-flowered; pedicels 7–18(–21) mm; peduncle and pedicels papillate, often with reddish or dark papillae, and usually with sparse small scurfy to flat-stellate scales; bracteoles scaly. Sepals (4–)5–6(–6.8) mm, usually reflexed at least after anthesis, occasionally not, bearing small stellate trichomes or scales; petals 6.5–9.5 × (3.8–)4.5–6.5 mm; corona 1–1.5 mm, not narrowed above ovary; anthers 0.8–1.1(–1.3) mm; style 1.5–3(–4) mm, the lower portion papillate and sometimes bearing a few short trichomes; style branches (1.2–)1.5–2.5 mm, papillate; ovary densely papillate, possibly becoming more sparsely papillate post-anthesis. Fruit not seen.

Distribution, habitat, and phenology. *Dombeya decanthera* subsp. *latipetala* is native to littoral forests of southeastern Madagascar; it has been reported to occur on basalt and from elevations of 21–72 m. It flowers in August through October; immature fruit has been collected in September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya decanthera* subsp. *latipetala* is noted as Vulnerable or VU, D. This subspecies does occur in a protected area, but there may be as few as five distinct populations, all relatively close geographically and, therefore, vulnerable to stochastic events.

Vernacular name. Hafotra [à petites feuilles] (*Service Forestier 12391*).

Discussion. *Dombeya decanthera* subsp. *latipetala* differs from *D. decanthera* subsp. *farafanganica* in that the leaves are frequently ovate, the marginal teeth are usually well defined and conspicuous, and secondary veins usually run to tooth apices; the inflorescence has fewer flowers on average, and the flower may be on average somewhat larger, with more consistently broad petals. *Applequist et al. 249* is identified as a probable hybrid between *D. decanthera* subsp. *latipetala* and *D. australis* subsp. *grandiflora*, both of which occur at Manombo. It has relatively large, broadly elliptical leaves but is virtually glabrous throughout, the latter state typical of *D. australis*.

The wood is used for poles and posts (*Service Forestier 16200*).

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** Atsimo-Atsinanana, Vohipaho, *Andriamihajarivo et al. 1683* (MO); Atsimo-Atsinanana, Vohipaho, *Andriamihajarivo et al. 1736* (MO); Atsimo-Atsinanana, Vohipaho, *Applequist et al. 255* (MO, P, TAN, US), *Applequist et al. 257* (MO, P, TAN, US); Atsimo-Atsinanana, Manombo, *Applequist et al. 263* (MO, P, TAN, US); Atsimo-Antsinanana, Manombo, *Rabarimanarivo et al. 65* (P); Manombo, *Rakotonirina et al. 277* (MO); Marimpananihy, Farafangana, *Service Forestier 16200* (MO, P); Manombo, Farafangana, *Service Forestier 23652* (MO, P).

Probable hybrid specimen. MADAGASCAR. **Fianarantsoa:** Farafangana, Manombo, *Applequist et al. 249* (MO, P, TAN, US).

6. Dombeya lavasoensis Arènes, Candollea 16: 395–396. 1958. TYPE: Madagascar. Toliara: forêts ombrophiles du massif du Lavasoa (au N de la baie des Galions), vers 150 m, Feb. 1955 (fl., fr.), *Service Forestier 11821* (holotype, P!; isotypes, P [2]!, TAN not seen, TAN image!).

Shrubs; twigs dark to very pale grayish brown, the youngest pilose with long (0.5–1 mm) white trichomes; stipules relatively persistent, very narrowly deltoid, 1–4 mm, sparsely pilose; stipule scars on young twigs crescent-shaped to hemielliptical, not prominent or conspicuously colored. Leaves elliptical to ovate, 3–6.7 × 1.7–3.5 cm; petiole 5–10(–15) mm, pilose; base rounded, often slightly asymmetrical to very shallowly cordate; apex acute; margins irregularly denticulate to serrulate or crenulate, glands apparently absent; both surfaces pilose, with occasional stellate trichomes; basal veins 5; secondary veins above base 5 to 7 per side, sometimes approaching craspedodromous, inconspicuous on adaxial surface; domatia absent. Flowers solitary, axillary near ends of branches, few in number; pedicels (8–)10–24 mm, possibly elongating in fruit, pilose; bracteoles frequently persistent past anthesis, lanceolate or narrowly deltoid, 2–4 mm, sparsely pilose, 2 borne close beneath flower with one often slightly lower. Sepals 6–7 mm, not reflexed, pilose, persistent in fruit; petals white, 8–9.5(–11) × 7–8(–9) mm, broadly obovate, prominently asymmetrical; corona 1.5–1.8 mm; stamens 15; filaments 1–2.5 mm; anthers 0.7–0.9 mm; staminodes narrowly spatulate, 4.3–4.7(–5.5) mm; style 5.5–6 mm; branches 3, 1.5–2 mm; ovary densely pubescent with large flattened stellate trichomes. Fruit pale to dark brown, shallowly lobed, 5–6 mm high, 7–10 mm diam., with few persistent stellate trichomes; seeds at least 2 per locule, suborbicular, 3–3.5 mm, reddish brown, mottled.

Distribution, habitat, and phenology. *Dombeya lavasoensis* has been collected from forests near the summits of granite massifs in extreme southeastern Madagascar; the only recorded altitude is 150 m. It flowers and fruits from December to February; mature or nearly mature fruits may be found on flowering branches.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya lavasoensis* is noted as Endangered or EN B1ab(iii)+2ab(iii). Only two localities are known; neither are protected and both are, therefore, subject to habitat degradation, and no recent collections have been made.

Discussion. *Dombeya lavasoensis* may be closely related to *D. decanthera*; they share elliptical to ovate leaves and varying degrees of pilose pubescence. However, the leaf marginal glands of *D. lavasoensis* are either extremely inconspicuous or entirely absent, and up to six seeds per fruit may mature. Neither condition is usual in *Dombeya* sect. *Decastemon*, though the fruits of many species are unknown. Its placement in this series, and even in this section, may be questionable; solitary flowers could have been derived from either an umbellate or a cymose inflorescence, though no species in *Dombeya* sect. *Xeropetalum* are particularly reminiscent of *D. lavasoensis*.

Additional specimen examined. MADAGASCAR. **Toliara:** massif of Vohitsiandriana, Ranopiso, *Service Forestier 28572* (P).

7. Dombeya pilosissima Appleq. & T. Andriam. TYPE: Madagascar. Atsimo-Atsinanana: Vangaindrano, Sianofana, Ambatomalama, forêt de Vohipa[h]o, 23°26′42″S, 047°30′57″E, 76 m, 22 Sep. 2009 (fl), *Razanatsima & Andriamihajarivo 776* (holotype, MO!; isotypes, P!, TAN not seen). Figure 1.

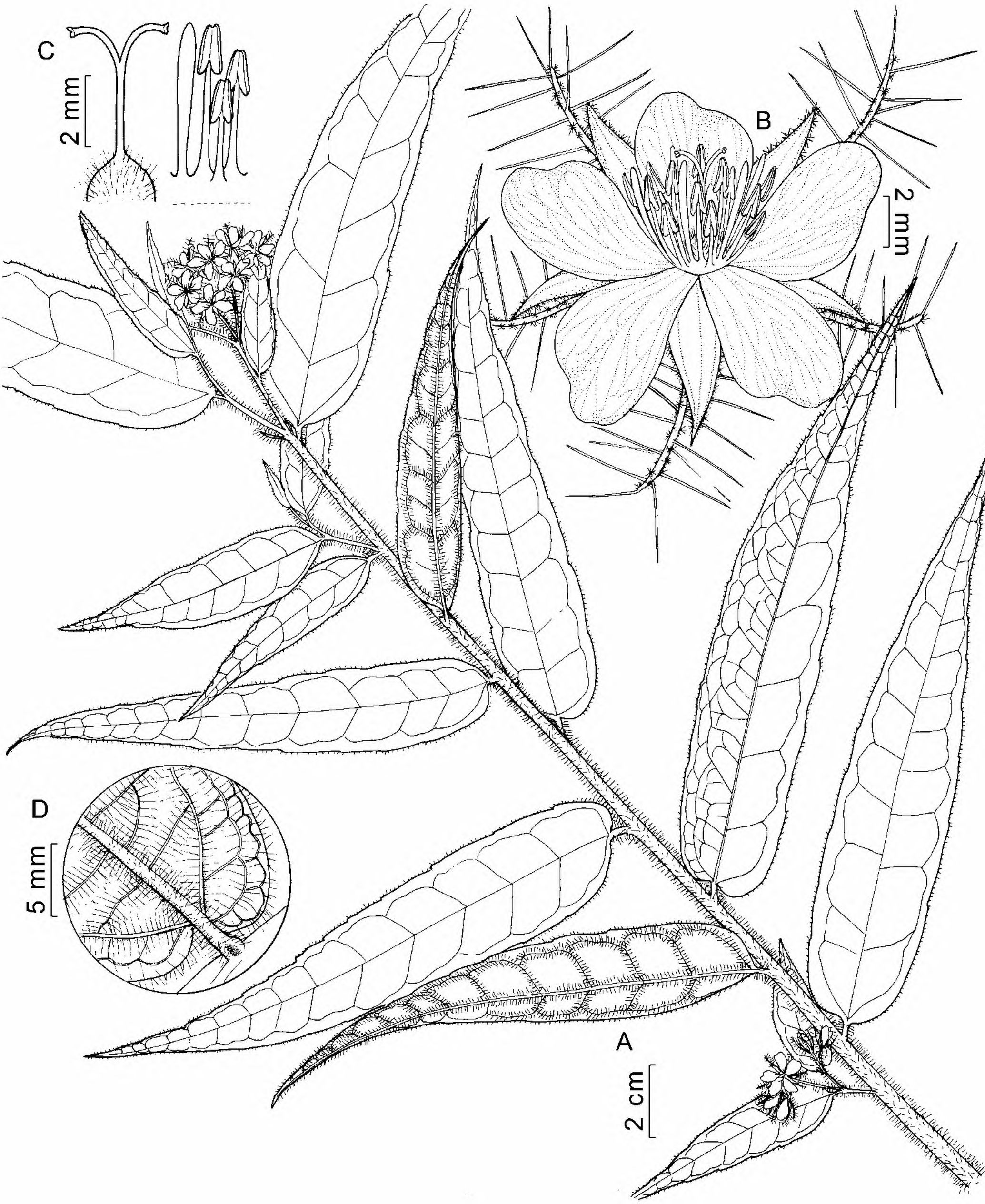


Figure 1. *Dombeya pilosissima* Appleq. & Bosser. —A. Habit. —B. Flower. —C. Gynoecium. —D. Abaxial leaf surface. A–D from *Razanatsima & Andriamihajarivo 776* (MO).

Diagnosis. Distinguished from *Dombeya lavasoensis* Arènes by narrowly lanceolate leaves, 13–16.5 cm long with shorter (4–5 mm) petioles and secondary veins 10 or more per side, very prominent beneath, inflorescences small, few-flowered cymes, flowers smaller (sepals 4–5 mm, petals 5–6.5 mm, corona 0.5 mm, style 1.5–3 mm) with sepals acuminate, petals narrower and less strongly asymmetrical.

Small tree to 3 m; twigs tan, the youngest pilose with very long (2.5 mm) white trichomes; stipules persistent, linear, 5.5–9 mm, pilose; stipule scars not seen. Leaves narrowly lanceolate, 13–16.5 × 2.3–3.5 cm; petiole 4–5 mm, pilose; base moderately oblique; apex narrowly acute; margins shallowly denticulate-crenulate, glands apparently absent; both surfaces long-pilose, with trichomes borne along veins includ-

ing tertiary and smaller veins; basal veins 5; secondary veins above base 10 or more per side, inconspicuous on adaxial surface, very prominent on abaxial surface; domatia absent. Flowers borne in small 2- to 10-flowered dichotomizing cymes 2.1–6 cm long; peduncle 1.2–2 cm, pilose; pedicels ca. 3–6 mm, pilose; bracts linear, 2.5–4 mm, pilose; bracteoles persistent, linear, 4.5–6 mm, pilose. Sepals 4–5 mm with acuminate apices, partly reflexed, stellate, pinkish; petals white, 5–6.5 × 3.2–3.5 mm, obovate, moderately asymmetrical; corona 0.5 mm; stamens 15; filaments 1.2–2 mm; anthers 0.7–1.1 mm, yellow; staminodes narrowly spatulate, 3–4.5 mm; style 1.5–3 mm; branches two, 0.8–1.3 mm; ovary densely stellate-pubescent. Fruit unknown.

Distribution, habitat, and phenology. *Dombeya pilosissima* has been collected in the sublittoral humid forest of Vohipaho [also called Vohipeno] in southeastern Madagascar at a recorded altitude of 76 m. The type specimen was flowering in September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya pilosissima* is noted as Endangered or EN B1ab(iii)+2ab(iii). There has been significant collection in remaining low-altitude forests in the region, so the fact that no other specimens of this very distinctive species are known indicates that it is geographically restricted and probably quite rare. Its habitat is under threat from human activity.

Etymology. *Dombeya pilosissima* is named for the very unusual dense, long-pilose indument on most organs, comparable in *Dombeya* subg. *Xeropetalum* only to that of *D. lavasoensis*. Tefy Andriamihajarivo (MO–Madagascar), one of the collectors of the type specimen, first determined this as a probable new species and hence shares authorship of the name.

III. Dombeya ser. **Mananarenses** Arènes, Candollea 16: 391. 1958. TYPE: *Dombeya mananarensis* Arènes. *Dombeya* subser. *Australes* Arènes, Candollea 16: 391. 1958. TYPE: *Dombeya australis* Scott-Elliot.

Dombeya ser. *Lepidotae* Arènes, Candollea 16: 390. 1958. TYPE: *Dombeya capuroniana* Arènes.

Young twigs glabrous, stellate, fimbriate-lepidote, scurfy, or pubescent; stipule scars hemielliptical to irregularly crescent-shaped or flattened deltoid, usually large, pale and at least slightly prominent, seldom small and not elevated. Leaves narrowly elliptical to oblong-elliptical or oblanceolate, less often to narrowly oblong, narrowly oblanceolate, oblong-oblanceolate, or obovate, or seldom tending to lanceolate; basal veins 1 to 5(to 7); secondary veins numerous or (4 to)6 to 10; domatia absent; petioles stellate to fimbriate-lepidote, glabrous, or slightly pubescent. Inflorescences umbellate, occasionally partly cymose or 1-flowered, stellate to scaly, fimbriate-lepidote, glabrate, or (in *D. mandenensis*) flocculent; peduncles (1.5–)7–50(–80) mm or rarely absent, usually longer than pedicels unless both are quite short. Petals broadly obovate to obovate or suborbicular, somewhat asymmetrical, not convex; stamens 10 to 15; staminodes ± oppositisepalous, longer than longest fertile filaments; ovary stellate to lepidote, rarely papillate.

Distribution and habitat. *Dombeya* ser. *Mananarenses* is mostly native to southeastern Madagascar, with one species each in Toamasina (*D. mangorensis*) and the extreme north (*D. capuroniana*). Littoral forest is the most common habitat, but some species occur in humid forests, transitional or dry forests, and bush or thickets; altitudes range from sea level to 1250 m.

Discussion. Six of the seven species included in *Dombeya* ser. *Mananarenses* are likely to form a natural group, as they share a very similar leaf morphology and a mostly southeastern distribution in Madagascar. Stipule scars on young twigs are broad, pale, and sometimes large and conspicuous, a feature widely distributed in the genus but developed to an extreme in some species of this series. *Dombeya capuroniana* is an outlier within the series, as it has a distinctly different leaf shape and is endemic to the extreme northern site of Montagne d'Ambre. It is placed in this series because its small but broad stipule scars and narrow leaves often broadest near the apex cause it to fit better here than in any other series as herein circumscribed. Arènes (1958) segregated *D. capuroniana* as the sole species within *Dombeya* ser. *Lepidotae* because the ovary is lepidote. However, given that indument is so variable in this group, this is a weak basis for description of series. The inclusion of *D. capuroniana* within *Dombeya* ser. *Mananarenses*, therefore, is done here for taxonomic convenience. *Dombeya* ser. *Mananarenses* is preferred as the name for the series because *D. capuroniana* is the least typical included species and because the name *Lepidotae* could be quite misleading, as most species are in no way lepidote.

KEY TO THE SPECIES OF *DOMBEYA* SER. *MANANARENSES*

1a. Twigs and petioles densely fimbriate-lepidote; basal leaf veins 1 ..... 9. *D. capuroniana*
1b. Twigs and petioles glabrous, stellate, or scurfy, seldom sparsely short-pubescent; basal leaf veins 3 to 5(to 7).
2a. Stipules persistent at twig apices; peduncle usually not much longer than pedicels (to [–14] mm) ..... 14. *D. rariflora*
2b. Stipules mostly caducous, though not always rapidly; peduncle usually longer than pedicels (rarely absent).
3a. Stipule scars on young twigs irregularly crescent-shaped to transversely obdeltoid, large and very conspicuous; leaves (8.5–)11–25 cm; pedicels stellate and often flocculent; endemic to Mandena ..... 11. *D. mandenensis*
3b. Stipule scars on young twigs broadly hemielliptical to irregularly crescent-shaped, moderately sized and often not conspicuous; leaves to 12 cm; pedicels glabrate to stellate or sparsely scaly, not flocculent.
4a. Twigs short-pubescent; basal leaf veins (3 to)5 to 7; petals 13–15 mm, filaments 2–4 mm, staminodes 5–7 mm; humid forest in Toamasina ..... 12. *D. mangorensis*
4b. Twigs stellate or glabrous; basal leaf veins 3 or 3 to 5; flowers variable in size, seldom with petals to 14 mm or staminodes to 6 mm, but filaments < 2 mm; southeastern Madagascar.
5a. Petioles reddish stellate; abaxial leaf surface sparsely stellate and minutely papillate to glabrate; basal veins 5 or 3; Mananara River basin ..... 10. *D. mananarensis*
5b. Petioles whitish stellate to glabrate; abaxial leaf surface sparsely stellate to glabrous, not papillate; basal veins 3.
6a. Young twigs glabrous; leaves 4–11.7 cm; peduncle (2.0–)3.5–5.5(–7.0) cm; bracteoles sometimes persistent; developing fruit subglobose, sparsely stellate ..... 8. *D. australis*
6b. Young twigs short-stellate; leaves 3.5–7 cm; peduncle 0.7–2.5(–3.5) cm (or absent); bracteoles caducous; developing fruit cylindrical, sometimes becoming papillate ..... 11. *D. ranofotsyensis*

8. Dombeya australis Scott-Elliot, J. Linn. Soc., Bot. 29: 8. 1891. TYPE: Madagascar. Toliara: woods, Fort Dauphin, Apr. (fl.), *Scott Elliot 2524* [*2668*] (holotype, K not seen, K image!; isotype, P!).

Tree to 8(–12) m tall, 10 cm diam., or large shrub; twigs grayish brown, the youngest dark brown, glabrous; stipules caducous or very rarely persistent, narrowly lanceolate, 2.5–6.5 mm, glabrous or glabrate; stipule scars on young twigs prominent, pale, roughly broadly hemielliptical. Leaves oblanceolate to narrowly elliptical or elliptical or rarely obovate, 4–11.7 × (1–)1.5–4(–4.7) cm; petiole 4–12(–22) mm, glabrous or glabrate with rare small stellate trichomes; base cuneate; apex cuspidate, acute, rounded, or short-acuminate; margins serrulate or rarely conspicuously serrate or crenulate, with glands located in tooth apices or marginal protrusions; youngest leaves sparsely stellate, mature leaves glabrous or glabrate; basal veins 3, the lateral weak; secondary veins above the base 6 to 10 per side or numerous, inconspicuous on adaxial surface; domatia absent. Inflorescences (1)2- to 6(7)-flowered; peduncle (2–)3.5–5.5(–7) cm, glabrous; pedicels 0.9–2.2(–2.7) cm, glabrous, or rarely with 1 to a few small scales on the pedicel and upper peduncle; bracteoles persisting in bud and sometimes into full flower, narrowly lanceolate to ovate, 2.5–4 mm, glabrate with rare small, stellate trichomes or glabrous, immediately beneath flower. Sepals 5.5–8(–9.5) mm, usually but not consistently reflexed, glabrate with very few small stellate trichomes; petals white, (6.5–)8–11(–12) × (4.5–)6–9(–10) mm, broadly obovate, usually ± asymmetrical, sometimes shallowly cleft; corona (0.5–)0.7–1.3 mm; stamens (10 to)15; filaments 0.5–1.5 mm; anthers 0.8–1.4 mm; staminodes linear, (3–)3.5–5(–6) mm; style 2–4(–5) mm, stellate on lower portion; style branches two, (1–)1.5–2.5(–3) mm, thick and flattened, if long then strongly curled; ovary stellate. Immature fruit subglobose, to at least 3.5 mm diam., dark brown, sparsely stellate; mature fruit not seen.

Discussion. Arènes (1958) recognized three subspecies within *Dombeya australis*, of which two are maintained; however, *D. australis* subsp. *geayi* (Hochr.) Arènes is not distinct from *D. australis* subsp. *australis*. The species' range extends from the extreme southeast, near Fort Dauphin, to points farther north around Farafangana. Populations from the northern portion of the range (*D. australis* subsp. *grandiflora*) have, on average, larger flowers but fewer flowers per inflorescence. Though both subspecies frequent littoral forests, they may have somewhat different ecological and substrate preferences. The type of *D. australis*, collected near Tôlanaro, has a young and damaged inflorescence but can be seen to have a 4-flowered inflorescence and a short style, with both features typical of the southern populations.

Original material for *Dombeya australis* was said by Hochreutiner (1926) to include the collections *Scott Elliot 2668* and *2524*, leading to confusion. The holotype at K was originally numbered *2524* but

later annotated "= *2668*." The protologue of *D. australis* cited only the number *2668* (providing additional evidence that the K specimen was used to prepare the publication), but the collection is more appropriately referred to as *2524*, the only number that appears on the P duplicate. Arènes (1958) described *2524* (K) as the lectotype, though he provided no indication that he thought any other original material had existed; this typification is superfluous.

KEY TO THE SUBSPECIES OF *DOMBEYA AUSTRALIS*

1a. Inflorescences (1- to)3- to 6(7)-flowered; sepals 5.5–6.3(–7.5) mm; petals 6.5–10.5 mm; style 2–2.8 mm; littoral and low humid forests of extreme southeast near Fort Dauphin .... 8a. subsp. *australis*
1b. Inflorescences 1- to 3(4)-flowered; sepals 6.5–8(–9.5) mm; petals (7–)8–12 mm; style 2.5–4.5(–5) mm; littoral forests along southeastern coast ..... 8b. subsp. *grandiflora*

8a. Dombeya australis Scott-Elliot subsp. **australis.**

Dombeya australis subsp. *geayi* (Hochr.) Arènes, Candollea 16: 393. 1958, syn. nov. Basionym: *Dombeya australis* var. *geayi* Hochr., Candollea 3: 31–32. 1926. TYPE: Madagascar. Toliara: province de Fort Dauphin, s.d. (fl., fr.), *F. Geay 6717* (holotype, P!; isotype, G not seen, G image!).

Inflorescences (1- to)3- to 6(7)-flowered. Sepals 5.5–6.3(–7.5) mm; petals 6.5–10.5 × 5.5–8 mm; style 2–2.8 mm.

Distribution, habitat, and phenology. *Dombeya australis* subsp. *australis* is usually found in littoral forests of extreme southeastern Madagascar, on sand; it is less often reported in low-elevation humid forest, sometimes along creeks, at elevations up to 105 m. It flowers from February through June; immature fruits have been collected in June.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya australis* subsp. *australis* is noted as Endangered or EN B1ab(iii)+2ab(iii). Fewer than five populations are known; the habitat has been unprotected and subject to degradation, although portions are reportedly to be protected in the future, and the populations are close enough together to be vulnerable to a single event.

Vernacular names. Berehoka (*Rajoharison & Tsiatrefy 83*), hafotrakarako (*Service Forestier 7428*).

Discussion. *Rabevohitra et al. 1894* has vegetative morphology typical of *Dombeya australis* subsp. *australis* but small, aberrant flowers, with unusually narrow petals and open appearance. It is not plausibly identifiable as a hybrid involving any other known species from the locality.

Additional specimens examined. MADAGASCAR. **Toliara:** Iabakoho, Antsotso Avaratra, *Birkinshaw et al. 1648* (MO); Fort Dauphin, Sainte Luce, *Decary 9931* (P), *9934* (P); Anosy, Antsotso, *Lowry et al. 6730* (MO); Mandena, *Rabevohitra 1798* (MO); Mandena, Mandromoromotra, *Rajoharison & Tsiatrefy 83* (MO); Fort Dauphin, Sainte Luce, 2 km W of Ambandrika, *Randrianasolo 342* (MO, P); Mandena, *Service Forestier 7428* (P); Bemangidy, N of Mahatalaky, *Service Forestier 11783* (P); Mandena, 24°57′S, 047°02′E, *Zarucchi et al. 7457* (P).

Hybrid or aberrant specimen. MADAGASCAR. **Toliara:** Tôlanaro, Mandena, *Rabevohitra et al. 1894* (MO, P).

8b. Dombeya australis Scott-Elliot subsp. **grandiflora** Arènes, Candollea 16: 393–394. 1958. TYPE: Madagascar. Farafangana: vestiges de forêt orientale, au S de Farafangana, le long de la route Farafangana–Manombo, 30 June 1954 (fl.), *Service Forestier 9209* (holotype, P!; isotypes, MO!, P [2]!, TEF not seen, TEF image!).

Inflorescences 1- to 3(4)-flowered. Sepals 6.5–8(–9.5) mm; petals (7–)8–12 × (4.5–)6–9(–10) mm; style 2.5–4.5(–5) mm.

Distribution, habitat, and phenology. *Dombeya australis* subsp. *grandiflora* is native to littoral forests of southeastern Madagascar, on laterite and basalt, or low-altitude humid forests on sand; it has been collected at elevations of 21–500 m. It appears to flower year-round; immature fruits have been collected in June and August.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya australis* subsp. *grandiflora* is noted as Vulnerable or VU B1ab(iii)+2ab(iii). Although several distinct populations are known, the area of occupancy is small, all populations are confined to a limited area, and most of the habitat is unprotected and subject to degradation.

Vernacular names. Hafopotsy (*Service Forestier 3802*), hafotra (*Service Forestier 14480*).

Discussion. The collection *Razakamalala et al. 2470* has short inflorescences and sparse stellate pubescence on twigs, inflorescences, and sepals; the leaves are narrowly elliptical, and the perianth is abnormally small. It appears intermediate between *Dombeya australis* subsp. *grandiflora* and *D. ranofotsyensis*, but the latter is not known from the area.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** Atsimo-Atsinanana, Manombo, *Applequist et al. 248* (MO, P, TAN); Atsimo-Atsinanana, Vohipaho, *Applequist et al. 256* (MO, P, TAN), *258* (MO, P, TAN); Atsimo-Atsinanana, Manombo, *Applequist et al. 262* (MO, P, TAN), *264* (MO, P, TAN), *265* (MO, P, TAN), *266* (MO, P, TAN); Iabomary, 40 km S of Farafangana, *Rabenantoandro et al. 421* (MO, P), *424* (MO, P); Farafangana, Manombo, 23°01′56″S, 047°42′07″E, *Rabenantoandro et al. 793* (MO); Vangnokely, Farafangana, *Service Forestier 3802* (P); Ifanadiana, Mananjary, *Service Forestier 14480* (P); between Farafangana and Manombo, *Service Forestier 23934* (P). **Toliara:** Anosy, Iabokoho, Antsotso, *Rajoharison et al. 181* (MO); Anosy, Fenoambany, *Razakamalala et al. 4603* (MO).

Probable hybrid specimen. MADAGASCAR. **Toliara:** Fort-Dauphin, Iaboko[ho], Antsotso, *Razakamalala et al. 2470* (MO, US).

9. Dombeya capuroniana Arènes, Candollea 16: 391. 1958. TYPE: Madagascar. Antsiranana: massif de la Montagne d'Ambre, rives du Grand Lac, 9 Oct. 1954 (fl., fr.), *Service Forestier 11271* (holotype, P!; isotypes, BR not seen, BR image!, K not seen, K image!, P [2]!, TAN not seen, TAN image!, TEF not seen).

Shrub or tree to 15 m; twigs pale grayish brown, the youngest lepidote with a dense coating of strongly fimbriate scales; stipules caducous, lanceolate, 1.5–3.5 mm, fimbriate-lepidote; stipule scars on young twigs pale, hemielliptical to narrowly elliptical but small, not at all prominent. Leaves narrowly oblong-oblanceolate to narrowly oblong or narrowly oblanceolate, (4.5–)6–10.8 × 1–1.8(–2.3) cm; petiole 3–11 mm, fimbriate-lepidote; base rounded to cuneate with extreme base rounded; apex acute or rarely rounded or emarginate; margins usually irregularly crenulate-serrulate near apex, otherwise subentire, glands inconspicuous and present only near apex; both surfaces sparsely lepidote with fimbriate scales; basal veins 1 or seldom 3, with the outer very weak; secondary veins numerous, weak, mostly reticulodromous except near apex, visible on adaxial surface; domatia absent. Inflorescences 1- to 4(to 7)-flowered, occasionally appearing at least partly cymose; peduncle (1.2–)2–4.6 cm; pedicels 5–15 mm; peduncle and pedicels fimbriate-lepidote; bracteoles caducous, occasionally persisting in flower, borne slightly below flower, ovate to lanceolate, 1–1.5(–2) mm, sparsely lepidote. Sepals 4.5–6.8 mm, sometimes reflexed, lepidote; petals white, 7–9.5 × 5–8 mm, broadly obovate, moderately asymmetrical; corona 0.5–1.7 mm; stamens 10; filaments 0.8–2 mm; anthers 0.6–1 mm; staminodes linear to narrowly spatulate, 3–3.5 mm; style (1.5–)3–3.5 mm, basally lepidote; style branches two or three, 1–2 mm, variably shaped; ovary lepidote. Developing fruit roughly globose or broadly ellipsoid, to 5 mm diam., pale, lepidote; possibly only 1(or 2) seeds developing per fruit, irregularly ellipsoid, pale brown, to at least 3 mm; mature fruit not seen.

Distribution, habitat, and phenology. *Dombeya capuroniana* is endemic to Montagne d'Ambre in northern Madagascar; the reported altitude range is 1100–1250 m. It flowers in June through October; immature fruits have been collected in October.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya capuroniana* is noted as Vulnerable or VU, D. This species is known only from the area of Montagne d'Ambre; it is, therefore, susceptible to natural disasters, though its habitat is protected, and the paucity of collections suggests that it is rare.

Discussion. *Dombeya capuroniana* is distinctive for its very narrowly oblanceolate, often more or less oblong leaves and fimbriate-lepidote indument throughout. Some similarities are observed between this species and the similarly lepidote *D. andrahomanensis* Arènes (the sole species Arènes placed within *Dombeya* ser. *Squamigerae*). Both have a single basal leaf vein, numerous weak secondary veins, and sometimes umbelliform-cymose inflorescences (though that is seen as an aberration in a number of other species). However, *D. andrahomanensis* has much narrower stipule scars, short-peduncled inflorescences, and typically narrowly elliptical leaves. It is, therefore, not possible to presume a close relationship between the two; the true affinities of both species are uncertain.

Additional specimens examined. MADAGASCAR. **Antsiranana:** Montagne d'Ambre PN, *Andrianantoanina & Bezana 151* (MO, P); forêt d'Ambre, *Perrier de la Bâthie 17732* (P).

10. Dombeya mananarensis Arènes, Candollea 16: 400. 1958. TYPE: Madagascar. Toliara: bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, entre Ampahiso et Mahamavo (gneiss), 500–800 m, Jan.–Feb. 1934 (fl.), *H. Humbert 13758* (holotype, P!; isotypes, BR not seen, BR image!, K [2] not seen, K [2] images!, MO!, P [3]!, PRE not seen, PRE image!, TAN not seen, TAN image!).

Tree; twigs grayish brown, the youngest reddish and finely stellate; stipules caducous, lanceolate-acuminate, 2.5–4 mm, sparsely stellate to glabrous;

stipule scars on young twigs prominent, pale or conspicuously darkened, hemielliptical. Leaves narrowly elliptical to narrowly oblong-elliptical or lanceolate, 4–7 × 1.4–2.5 cm; petiole (7–)11–20 mm, densely stellate with fine reddish trichomes; base rounded, often slightly asymmetrical; apex acute; margins serrulate with small, often rounded teeth with glands located in tooth apices; abaxial surface sparsely pubescent with fine, mostly stellate trichomes and tiny papillae or glabrate, adaxial surface glabrous; basal veins 5, the outermost weak, or 3; secondary veins above the base 6 to 8 per side, weak, visible on apical surface; domatia absent. Inflorescences (1)2- to 4-flowered; peduncle 1.5–5.1 cm; pedicels 4–9(–13) mm; peduncle and pedicels sparsely reddish stellate; bracteoles caducous, ovate, 1.2–2.3 mm, glabrous, borne immediately or very slightly below flower. Sepals 5.4–5.8 mm, reflexed, shallowly fused at base, sparsely stellate, sometimes becoming glabrous; petals white, (8–)9.5–11.7 × 6–8(–10) mm, broadly obovate, somewhat asymmetrical; corona 1.5–2 mm; stamens 10; filaments 0.5–1.2 mm; anthers pale yellow, 0.8–1 mm; staminodes linear, 3.5 mm; style 3–3.5 mm; branches three, 1.5 mm, curved; ovary with dense indument of large flattened stellate trichomes.

Distribution, habitat, and phenology. *Dombeya mananarensis* has been collected from a single location in southeastern Madagascar, on gneiss at an elevation of 500–800 m; it was flowering in January or February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya mananarensis* is noted as Data Deficient or DD. Although the species is known only from the type collection, botanical specimens from the area of the Mandrare are scarce, except for Humbert's collections, and few inferences about habitat quality or population size can be made.

Discussion. *Dombeya mananarensis* most closely resembles *D. ranofotsyensis*, as both species have leaves of modest size with a rounded base, sparse stellate indument on most parts, and relatively large flowers. However, the indument is in large part reddish; the leaves sometimes tend to be lanceolate and are somewhat asymmetrical at the base with often five basal leaf veins; the abaxial leaf surface is somewhat papillate as well as stellate; the peduncles are unusually long; the style is unusually long and 3-branched; and the ovary bears large flat-stellate trichomes.

11. Dombeya mandenensis Arènes, Candollea 16: 398–399. 1958. TYPE: Madagascar. Toliara: Mandena, à 12 km au N de Fort Dauphin, forêt sublittorale, sur sables, July 1954 (fl.), *Service Forestier 9223* (holotype, P!; isotypes, K not seen, K image!, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Small tree to 8 m, to 25 cm diam., sometimes shrubby or much-branched; twigs thick, grayish, glabrous; stipules deltoid, 4–6 mm, reddish brown, mostly glabrate, sometimes with a pubescent keel; stipule scars on young twigs very prominent, pale, irregularly crescent-shaped to transversely obdeltoid, to 4.2 mm broad. Leaves narrowly elliptical to oblong-elliptical, occasionally tending to oblanceolate or lanceolate especially when young, (8.5–)11–25 × (2.3–)2.7–5 cm; petiole (3–)4–6 mm, initially stellate, sparsely scurfy-pubescent to glabrous at maturity; base ± cuneate, sometimes rounded at extreme base; apex acute to rounded or emarginate; margins serrulate with inconspicuous glands in tooth apices; both surfaces densely stellate in very young leaves, usually becoming glabrous, occasionally remaining sparsely stellate especially beneath; basal veins 3, the lateral weak; secondary veins above the base numerous, visible though not conspicuous on adaxial surface; domatia absent. Inflorescences (2- to)4- to 12-flowered; peduncle sometimes virtually absent, sometimes 1–5.4 cm, at least sparsely stellate, sometimes stellate with white flocculent coating; pedicels 5–12(–19) mm, stellate, often with white flocculent coating; bracteoles caducous or sometimes persistent to anthesis, ovate with often cuspidate apex, 3–4.5 mm, reddish brown, scurfy-pubescent basally with broad glabrous margins, borne immediately beneath flower. Sepals 6.8–9.5 mm, sometimes with a curved tip, not reflexed or reflexed, stellate; petals white, 8–11 × 5–7.5(–9) mm, broadly obovate, at least somewhat asymmetrical; corona 0.6–1 mm; stamens (10 to)15; filaments white, 1.5–3 mm; anthers orange, 0.9–1.5 mm; staminodes linear, 5–7 mm; style 4–5 mm; style branches three, 1.5–2 mm, rarely divided to ovary and to 4 mm; ovary densely stellate. Fruit densely stellate-pubescent, subglobose, sometimes vertically compressed, shallowly lobed, 5–10 mm diam.; seeds probably 3 per fruit, reddish brown, irregularly shaped, to 3.3 mm, roughly triangular in cross-section, shriveled and with deep wrinkles (mature seeds possibly not seen).

Distribution, habitat, and phenology. *Dombeya mandenensis* is native to littoral and sublittoral forests of extreme southeastern Madagascar, on sand at

elevations of 0–25 m. It appears to flower, and possibly set fruit, year-round.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya mandenensis* is noted as Vulnerable or VU B1ab(iii)-2ab(iii). Only two distinct populations exist (around Mandena and Sainte Luce) in a very small geographic area; the habitat has suffered significant fragmentation and continuing degradation, although it is reportedly to be protected in the future.

Vernacular names. Berehoka (*Rabenantoandro et al. 351*, *Ramison 214*, *Ramison & Armand 370*), savalengo (*Decary 4169*).

Discussion. *Dombeya mandenensis* is a highly localized endemic species distinctive for features including the leaf size, unusual stipule and bracteole morphology, very conspicuous large, elongated, and raised stipule scars, and whitish pubescence on young parts and inflorescences, often accompanied by a flocculent coating. Peduncles in this species can be far longer than the pedicels or virtually lacking. The flowers are reported to have an odor of jasmine (*Dumetz et al. 785*).

Rabevohitra 2051 has elliptical leaves to 3 cm broad but only 6–7.5 cm long; all parts are glabrous or glabrate, except that the ovary is sparsely stellate. The stipule scars are smaller than usual for *Dombeya mandenensis*; the inflorescence is more slender and the flowers smaller; and the sepals are reflexed. This specimen is plausibly interpreted as a hybrid of *D. mandenensis* and *D. australis* subsp. *australis*, both of which occur in the vicinity.

Additional specimens examined. MADAGASCAR. **Toliara:** Fort Dauphin, *Decary 4169* (P); Mandena, *Dorr et al. 3991* (MO, P); Mandena, *Dumetz et al. 658* (MO), *734* (MO, P), *785* (P); Sainte Luce, *Faliniaina et al. 13* (MO); Mandena, *McPherson & Dumetz 14327* (MO, P); Sainte Luce, *McPherson et al. 14833* (MO); Sainte Luce, *Rabenantoandro et al. 351* (MO); Anosy, Mandena, *Rabenantoandro 1768* (MO); Mandena, *Rabevohitra et al. 1757* (MO); Mandena, *Rabevohitra 2021* (P); Anosy, Sainte Luce, *Raharimampionona 75* (P); Anosy, Mandena, *Ramison 214* (MO); Anosy, Mandena, *Ramison & Armand 370* (MO); Matalaky [Sainte Luce], *Randrianaivo et al. 862* (MO, P); Mandena, *Randrianasolo 577* (MO, P); Sainte Luce, *Razakamalala et al. 4329* (MO, US).

Hybrid specimen. MADAGASCAR. **Toliara:** Manafiafy [Sainte Luce], *Rabevohitra 2051* (MO).

12. Dombeya mangorensis Arènes, Candollea 16: 399–400. 1958. TYPE: Madagascar. Toamasina: moyenne vallee du Mangoro, 10 Sep. 1942 (fl.), *R. Decary 18531* (holotype, P!; isotypes, BR not seen, BR image!, K not seen, K image!).

Small tree with long lianoid branches; twigs grayish brown, the youngest pubescent; stipules caducous, narrowly lanceolate to linear, 2–4 mm, stellate; stipule scars on young twigs small but slightly broadened and often pale. Leaves oblong to oblanceolate, 6–10.5 × 2.5–4.6 cm; petiole 1–5(–8) mm, bearing small branched or unbranched trichomes, becoming glabrate; base shallowly cordate to rounded; apex usually cuspidate, occasionally emarginate; margins irregularly crenulate to crenate-serrulate or subentire, with inconspicuous glands located in tooth apices or small rounded projections; both surfaces usually glabrous at maturity, abaxial surface sometimes with few small stellate trichomes mostly on midrib; basal veins (3 to)5 to 7; secondary veins above base numerous or 7 to 10 per side, visible on adaxial surface; domatia absent. Inflorescences (1)2- to 6-flowered, rarely perhaps cymose; peduncle (3–)4.5–8 cm; pedicels 6–14 mm; peduncle sparsely stellate-scaly, pedicels more densely stellate; bracteoles caducous, ovate, 4 mm, stellate, borne close beneath flower. Sepals 7–9 mm, narrow, mostly not reflexed, densely stellate; petals 13–15 × 10–12 mm, broadly obovate, asymmetrical; corona 1.3–1.4 mm; stamens ca. 15; filaments 2–4 mm; anthers 0.8 mm; staminodes linear, 5–7 mm; style 6–7 mm; branches two or three, 2–2.5 mm, flattened, tightly curled; ovary densely short-stellate (almost long-fimbriate lepidote).

Distribution, habitat, and phenology. *Dombeya mangorensis* is known only from the vicinity of the Mangoro River in eastern Madagascar, presumably in humid forest; flowering material has been collected in September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya mangorensis* is noted as Critically Endangered or CR B1ab(iii)-2ab(iii); only one locality is known, from which two specimens were simultaneously collected, and no further collections have been made. Unprotected forests in the area are under great threat from human activity.

Discussion. *Dombeya mangorensis* is the only species of *Dombeya* ser. *Mananarenses* that occurs in Toamasina. It has larger flowers than any other species of the series, five to seven basal leaf veins, and pubescent indument on the young twigs.

Additional specimens examined. MADAGASCAR. **Toamasina:** Mangoro, *Decary 18530* (P).

13. Dombeya ranofotsyensis Arènes, Candollea 16: 392. 1958. TYPE: Madagascar. Toliara: Ranofotsy, distr. de Fort Dauphin, pentes gneissiques, 29 July 1932 (fl., fr.), *R. Decary 10177* (holotype, P!; isotypes, B not seen, B image!, BR not seen, BR image!, P!).

Small tree or large shrub; twigs grayish to dark brown, the youngest ± short-stellate; stipules caducous, lanceolate, 1.5–2 mm, glabrous or sparsely stellate; stipule scars on young twigs dark or pale, hemielliptical to narrowly crescent-shaped. Leaves narrowly elliptical to oblanceolate or narrowly obovate, 3.5–7 × 1.1–3.2 cm; petiole 5–12(–17) mm, short-stellate or glabrate; base rounded to cuneate; apex rounded to acute; margins crenulate to subentire or serrulate with teeth usually rounded, glands usually in or near tooth apices or projecting slightly from margin; youngest leaves sparsely stellate, mature leaves glabrate with few small stellate trichomes, mostly along veins and at base; basal veins 3; secondary veins above the base (4 to)6 to 10 per side or numerous, visible on adaxial surface; clusters of trichomes sometimes present in clefts in axils of basal leaf veins, but no definite domatia present. Inflorescences 1- to 3-flowered; peduncle 0.7–2.5(–3.5) cm or rarely absent in single-flowered inflorescences, glabrous or sparsely stellate; pedicels 5–12 mm, glabrous or sparsely stellate; bracteoles caducous, ovate, 1–1.8 mm, glabrous, borne immediately beneath flower. Sepals 4.5–7 mm, almost all reflexed, glabrate with very few small stellate trichomes; petals white or yellow to orange (probably only post-anthesis), 8–12.5(–14) × 5.4–9.5(–11) mm, broadly obovate to suborbicular, moderately asymmetrical; corona 1.3–2.4 mm; stamens 10(to 15); filaments 0.5–1.5 mm; anthers 0.7–1.1 mm; staminodes linear, 3.5–4.5 mm; style 1–2.5 mm; style branches two, 1.5–2.5 mm, ± curled; ovary stellate. Fruit cylindrical, to at least 5–7 mm high × 2.5 mm diam., pale, sparsely stellate to papillate, petals remaining closed around developing fruit; developing seeds 1 or 2 per fruit, 0.8–0.9 mm, brown, suborbicular, somewhat asymmetrically compressed (probably no mature fruits seen).

Distribution, habitat, and phenology. *Dombeya ranofotsyensis* is native to a limited portion of extreme southeastern Madagascar but is reported in habitats ranging from humid and transitional forest to dry forest, bush, and thickets; it is known to occur on gneiss. The species has been collected from elevations of 1–779 m. It flowers from December through July; fruits, all possibly immature, have been collected in May, July, and December.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ranofotsyensis* is noted as Vulnerable or VU B1ab(iii)+2ab(iii). Six distinct populations are known, but all are in a small area that could be affected by a single event; natural habitat in the area, though partly protected, has been degraded.

Vernacular name. Hatapiso (*Birkinshaw et al. 425*).

Discussion. *Dombeya ranofotsyensis* closely resembles and is presumed to be closely related to *D. australis*, from which it differs in features including its more elliptical leaf shape with generally crenulate rather than serrulate margins, pubescence on most plant organs, shorter and fewer-flowered inflorescences, smaller and less persistent bracteoles, and the conformation of the developing ovary (cylindrical, rather than subglobose). The peduncle of *D. ranofotsyensis* is usually, but not always, longer than the pedicels, whereas the peduncle of *D. australis* is usually more than 3.5 cm long and virtually always exceeds the pedicels.

The wood is reportedly used for construction (*Birkinshaw et al. 425*), although the plant does not attain a large size.

The collection *Eboroke 996* resembles *Dombeya ranofotsyensis* but has filaments to 6.5 mm and equal to or exceeding the staminodes, a long corona narrowed above the ovary, a long style with short branches, unusually narrow petals, and leaves with oblique leaf bases and short-acuminate or cuspidate apices. This morphology can be fully explained as the result of hybridization between *D. ranofotsyensis* and *D. tulearensis* Arènes, both of which occur at Andohahela National Park.

Additional specimens examined. MADAGASCAR. **Toliara:** Anosy, Andohahela, mont Apiky, *Andriamihajarivo et al. 1146* (MO); Tsimelahy, Andohahela, parcelle 2, path E from Tsimelahy to Ambohibory massif, *Birkinshaw et al. 425* (P); Antanimora, Fort Dauphin, *Decary 4314* (MO, P); Baie des Galions (Ranofotsy), *Humbert 29019* (P [2]); Anosy, Ranopiso, SW of Ankilivalo, *Rakotovao et al. 5493* (MO); Andohahela (parcel 3), Ankazofotsy, *Randriamampionona 991* (P); Analamatsaka (parcel 3), Andohahela, *Ratovoson et al. 98* (MO, P); 10 km NE of Tsimelahy, Ranopiso, Fort Dauphin, *Ravololonanahary et al. 93* (MO, P); Italy (Baie de Ranofotsy), Fort Dauphin, *Service Forestier 20504* (MO [2], P [3]).

Hybrid specimen. MADAGASCAR. **Toliara:** Andohahela, 8 km W of Ambatoabo, Vohidafa, *Eboroke 996* (P).

14. Dombeya rariflora Arènes, Candollea 16: 397–398. 1958. TYPE: Madagascar. Toliara: falaise cotière NW du Cap Sainte-Marie, vers Lavano-

no, bush xérophile sur calcaire, 1–150 m, 8 Mar. 1955 (fl.), *H. Humbert 29320* (holotype, P!; isotypes, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Tree to 7 m, with DBH to 20 cm, or shrub to 4 m; twigs grayish brown, the youngest sparsely pubescent with small scurfy stellate trichomes to glabrate; stipules persistent at twig apices, narrowly deltoid-acuminate, (3–)5–8 mm, sparsely stellate to glabrate; stipule scars on young twigs usually prominent, pale or occasionally dark, irregularly crescent-shaped to broadly hemielliptical. Leaves narrowly elliptical, occasionally tending to oblanceolate, (3.7–)5.5–12.5 × (1.3–)1.8–3.5 cm; petiole (3–)4–6(–10) mm, sparsely stellate to glabrate; base narrowly rounded to cuneate; apex acute to rounded; margins apically serrulate to crenulate-serrulate with inconspicuous glands in apices of teeth; abaxial surface glabrous to sparsely stellate, adaxial surface glabrous; basal veins 3, the lateral weak; secondary veins above the base numerous or 7 to 10 per side, often inconspicuous on adaxial surface; domatia absent. Inflorescences (1-to)3- or 4-flowered; peduncle 1.5–6(–14) mm, sparsely stellate; pedicels 1–4(–9) mm, fairly thick, often somewhat flattened and angular, at least sparsely stellate; bracteoles persistent, narrowly deltoid, linear to subulate with a broad base, or less often broadly deltoid-acuminate, (3–)5–7 mm, sparsely stellate, borne immediately beneath flower. Sepals 4–6.5(–7.4) mm, not reflexed, stellate; petals white, 4.5–6.1(–6.5) × 2.8–3.6(–6) mm, obovate with asymmetrical apex or occasionally broadly obovate; corona 0.5–0.8 mm; stamens 10; filaments 0.7–1.5 mm; anthers 1–1.4 mm; staminodes linear to narrowly spatulate, 2.5–4 mm; style 1.5–3 mm; style branches three, 1–2 mm, spreading or curled; ovary densely white-stellate with long-armed trichomes. Fruit densely stellate, greenish when young, subglobose, shallowly lobed and vertically compressed, 4–7 mm diam.; seeds 3 to 6 per fruit, pale to medium brown, broadly ovoid to ellipsoid, 2.5–3.5 mm, strongly laterally compressed (mature seeds possibly not seen).

Distribution, habitat, and phenology. *Dombeya rariflora* is native to littoral forest and bush near sea level in extreme southeastern Madagascar, on sand or rarely limestone. The species has been collected at elevations to 100 m. It usually flowers from January to March, though flowering collections have been made in June and October; fruits have been collected from February to April.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya rariflora* is noted as Vulnerable or VU, D. All recent collections have come from a single locality, the littoral forest of Petriky, part of which is putatively to be protected, although it does not yet have formal status as a protected area. Repeated recent collections demonstrate the persistence of that population but not that of the type locality near Cape Sainte Marie (a protected area).

Vernacular names. Berehoka (*Randriatafika et al. 365*), mandoavato (*Randriatafika 711*), mandohavato (*Ramison 241*).

Discussion. *Dombeya rariflora* is distinguished by having usually very short peduncles and pedicels, persistent stipules subtending the small inflorescences, and rather sepaloid persistent bracteoles. Bracteoles that are both large and persistent are very unusual in *Dombeya* sect. *Decastemon*, and this character may suggest an affinity to *D. australis*, which has relatively large and persistent bracteoles (though less so than in *D. rariflora*).

Additional specimens examined. MADAGASCAR. **Toliara:** Fort Dauphin, Petriky, *Dumetz et al. 799* (MO, P); Fort Dauphin, Petriky, *Dumetz 1164* (MO); Tôlanaro, Petriky, *Gereau et al. 3210* (MO); Tôlanaro, Petriky, *Gereau et al. 3359* (MO, P); Baie des Galions (Ranofotsy), Fort Dauphin, *Humbert 28993* (P); Tôlanaro, *McPherson et al. 14767* (MO, P); Tôlanaro, Petriky, *Rabevohitra 2101* (MO, P); Anosy, Tôlanaro, Petriky, *Ramison 241* (MO); Petriky, Fort Dauphin, *Randriatafika et al. 73* (MO, P); Fort Dauphin, Petriky, *Randriatafika et al. 365* (MO, P); Anosy, Tôlanaro, Petriky, *Randriatafika 711* (MO).

IV. Dombeya ser. **Pentandrae** Appleq., ser. nov. TYPE: *Dombeya milleri* Appleq. & Bosser.

Domatia present in axils of secondary veins; stamens 5; staminodes opposite petals, broad and spreading; corona and filaments short; maturing ovary somewhat inflated with empty space inside before seeds develop.

Young twigs stellate to scaly stellate or fimbriate-lepidote; stipule scars irregularly hemielliptical, pale, sometimes slightly prominent, or stipules or basal portions of stipules persisting. Leaves elliptical or narrowly elliptical to ovate, lanceolate, or oblong-elliptical, or obovate; basal veins 3 to 5; secondary veins 3 to 5; domatia usually present in axils of secondary veins and sometimes also at base; petioles stellate to fimbriate-lepidote. Inflorescences umbellate, stellate, or fimbriate-lepidote; peduncles 0.5–20 mm, shorter or longer than pedicels. Petals broadly obovate to broadly obdeltoid, slightly to strongly asymmetrical, not convex; stamens 5; staminodes conspicuously oppositipetalous, longer than longest fertile filaments; ovary stellate, in one

species possibly papillate or scaly. Immature fruit, where known, becoming inflated before seeds develop.

Distribution and habitat. *Dombeya* ser. *Pentandrae* is native to deciduous forests in the extreme north of Madagascar at low altitudes (100–385 m).

Discussion. *Dombeya* ser. *Pentandrae* is described to encompass a group of three species whose floral morphology is unique within *Dombeya*, while not fitting into any related genus as presently defined. Skema's (2012) phylogeny suggests that this group may occupy a basal position. The fertile stamens are reduced to five and are clearly oppositisepalous. In contrast, almost all other species of *Dombeya* have 10 or more stamens, which are usually more or less oppositipetalous, though generally not conspicuously so due to the form of the androecium. The corona and filaments are unusually short, in two species being so reduced as to be almost entirely hidden by the ovary, and the staminodes broad and often spreading over the center of the petals. The style is divided to the base. Morphological synapomorphies, therefore, afford considerable confidence that this is a natural group. The first of the included species to be recognized was described only recently (Skema & Dorr, 2010), and two further species are newly described. Since some of the localities involved have been heavily collected, the paucity of collections suggests that the three species of *Dombeya* ser. *Pentandrae* are rare. *Dombeya ramiovensis*, which has five to 10 stamens, multiple pairs of domatia, and immature fruit with empty space inside, was herein placed in *Dombeya* ser. *Apikyenses* but might prove to be related to *Dombeya* ser. *Pentandrae*. It is not now placed within the latter series because the staminodes are oppositisepalous and linear, and the style is sometimes deeply divided but not to the base; other individually less important characters (e.g., relatively narrow petals, reflexed sepals, long corona and filaments) also bear more resemblance to less problematic species of *Dombeya* ser. *Apikyenses* than to the rather homogenous group of *Dombeya* ser. *Pentandrae*.

KEY TO THE SPECIES OF *DOMBEYA* SER. *PENTANDRAE*

1a. Leaf margins irregularly pinnately lobed and sinuate ..... 15. *D. gautieri*
1b. Leaf margins subentire to crenulate.
  2a. Leaves obovate with rounded to emarginate apices; petioles, leaves, and inflorescences fimbriate-lepidote to semi-stellate with flattened trichomes ..... 16. *D. milleri*
  2b. Leaves narrowly elliptical to lanceolate, oblong-lanceolate, or oblong-elliptical with acute apices; petioles, leaves, and inflorescences stellate ..... 17. *D. ratovosonii* Appleq.

15. Dombeya gautieri Dorr & Skema, Kew Bull. 65: 305. 2010. TYPE: Madagascar. Antsiranana: sous-préfecture de Vohemar, commune rurale de Daraina, Daraina, forêt de Solaniampilana–Maroadabo, 13°05.69′S, 049°34.89′E, 100 m, 11 Mar. 2004 (fl.), *L. Gautier et al. 4578* (holotype, US!; isotypes, G not seen, MO!, P not seen, TEF not seen).

Shrub to 2.5 m; twigs dark reddish brown, the youngest densely stellate; stipules persistent, subulate with broadened base, 2–3 or less than 1 mm, stellate, becoming glabrate; on young twigs stipule bases persist after stipules and leaves are lost. Leaves ovate to narrowly ovate, 3.3–5.7 × 2–2.9 cm; petiole 2–3 mm, densely stellate; base cuneate to rounded; apex acute to obtuse or rounded; margins irregularly pinnately lobed and sinuate, sparsely ciliate, with glands absent or very inconspicuous; adaxial surface sparsely pubescent with simple and 2-branched trichomes, stellate on veins; abaxial surface sparsely stellate; basal veins 1, the first pair of veins above the base weak; secondary veins above the base (4)5 per side, sometimes craspedodromous, often weakening sharply before margin, visible on adaxial surface; domatia present, small, roofed, basal and in axils of lower secondary veins. Inflorescences (1)2- or 3-flowered, often paired; peduncles 0.6–2 mm; pedicels 6–10 mm, longer than peduncle; peduncle and pedicels stellate; bracteoles sometimes persisting to anthesis, 0.5–1 mm, awl-shaped, stellate, borne immediately beneath flower. Sepals 3–4 mm, not reflexed at anthesis, stellate; petals white, 2.5–3 × 3.5–4 mm, broadly obovate, strongly asymmetrical; corona 0.5–0.6 mm; stamens 5; filaments 0.4–0.5 mm; anthers 0.5–0.8(–1) mm; staminodes white, lanceolate with a narrowed base, petaloid, 3–3.7 mm; styles 2, divided almost to ovary, 0.6–0.8 mm, glabrous; immature ovary papillate or possibly scaly stellate. Fruit unknown.

Distribution, habitat, and phenology. *Dombeya gautieri* is known only from the type collection, which was collected from a low-altitude (100 m) dry forest in northeastern Madagascar; it was flowering in March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya gautieri* is noted as Critically Endangered or CR B1ab(iii)-2ab(iii). The type locality is not protected, and since the area has been well collected in recent years, the

absence of other collections suggests that the population is very small.

Discussion. *Dombeya gautieri* was recently described by Skema and Dorr (2010), who noted a series of characters that distinguished it from all other then-recognized species of *Dombeya*, including its pinnately lobed leaves (with rare multiple domatia), stamens reduced in number to five, short corona and filaments, and unusually broad, spreading staminodes, which they termed petaloid. The staminodes, like those of two related species newly described below, are conspicuously oppositipetalous, whereas *Dombeya* is remarked for having usually (though not always consistently) more or less oppositipetalous stamens and oppositisepalous staminodes. Skema and Dorr considered the possibility of placement in some other genus; however, placement in any other recognized genus was not supportable on morphological grounds. *Dombeya milleri* and *D. ratovosonii* have a similar floral morphology in an even more extreme form, in which the corona is so short that it is completely concealed by the ovary; they do not share the very persistent stipules of *D. gautieri*.

16. Dombeya milleri Appleq. & Bosser, sp. nov. TYPE: Madagascar. Antsiranana: Montagne des Français, along trail from King's Lodge to ruins of fort, deciduous forest at summit on karst, 12°19′28″S, 049°20′14″E, 290 m, 19 Jan. 2003 (fr.), *J. S. Miller, W. Applequist, J. Rabenantoandro & R. Ranaivojaona 10695* (holotype, MO!; isotypes, G!, P not seen, TAN not seen, US not seen). Figure 2.

Diagnosis. Distinguished from *Dombeya gautieri* Dorr & Skema by obovate, unlobed leaves, staminodes narrower, corona and filaments shorter and hidden by ovary, ovary stellate.

Tree to 5 m; twigs grayish brown, the youngest fimbriate-lepidote or semi-stellate with flat long-fimbriate scales, the leaves somewhat congested toward twig apices; stipules caducous, lanceolate to deltoid, 1–2 mm, sparsely scaly stellate; stipule scars on young twigs irregularly hemielliptical to broadly hemielliptical, pale or seldom dark especially at twig apices, not or slightly prominent. Leaves numerous, obovate, 1.5–5.6 × 0.9–2.5 cm; petiole 1.5–6 mm, fimbriate-lepidote; base rounded to cuneate; apex shallowly emarginate to rounded with midrib sometimes projecting very slightly; margins subentire, with glands absent or few and inconspicuous; both surfaces sparsely fimbriate-lepidote to semi-stellate; basal veins 3(to 5), the outer usually weak; main secondary veins above base 3 to 5 per side, reticulodromous, usually visible but inconspicuous on adaxial surface; domatia sometimes present in axils of main secondary veins, seldom at base, small, roofed. Inflorescences 1 per node, 2- to 6-flowered; peduncle (1.5–)4–20 mm; pedicels 7–15 mm, sometimes curved shortly below flower, shorter or longer than peduncle; peduncle and pedicel sparsely fimbriate-lepidote to semi-stellate; bracteoles usually persistent, 1–1.8 mm, narrowly lanceolate-acuminate to awl-shaped, sparsely scaly stellate, borne immediately beneath flower. Sepals (1.5–)2–2.7 mm, not reflexed, scaly stellate; petals 4–6 × 4–6 mm, broadly obovate, apex truncate to mostly rounded and moderately asymmetrical, generally pressing open flat beginning shortly after anthesis and possibly rotate in living material; corona 0.2–0.4 mm, flattened and hidden by ovary; stamens 5, alternating with petals; filaments 0.2–0.4 mm, largely hidden by ovary; anthers 0.4–0.6 mm, deltoid; staminodes oppositipetalous, spatulate, 1.5–2.2 mm; styles 2, divided to ovary, 1.2–1.8 mm; ovary stellate. Immature fruit subglobose, to 2.5 mm diam., vertically somewhat compressed, stellate, with much empty space inside locules while developing ovules are still small; ovules 2 per locule, not winged; maturing seeds 1 per fruit, pale brown, broadly ellipsoid with irregularly concave sides, to at least 2 mm (possibly no mature seeds seen).

Distribution, habitat, and phenology. *Dombeya milleri* is endemic to Montagne des Français in extreme northern Madagascar. The newly described species occurs in deciduous forest on limestone and has been collected at 178 and 290 m in elevation. It flowers from December through February, with fruits collected in January and February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya milleri* is noted as Vulnerable or VU, D. The species is known to exist at only one locality, but the habitat is still in relatively good condition and is soon to be designated as protected.

Discussion. *Dombeya milleri* shares an unusual floral morphology with *D. gautieri* but shows more extreme reduction in the corona and filaments. The flowers are small and after anthesis almost always dry in an open position (a character that is also conspicuous in certain other broad-petaled species, notably *D. lecomtei*). *Razafitsalama 1199* has a few deformed budding structures with numerous linear sterile parts in leaf axils.

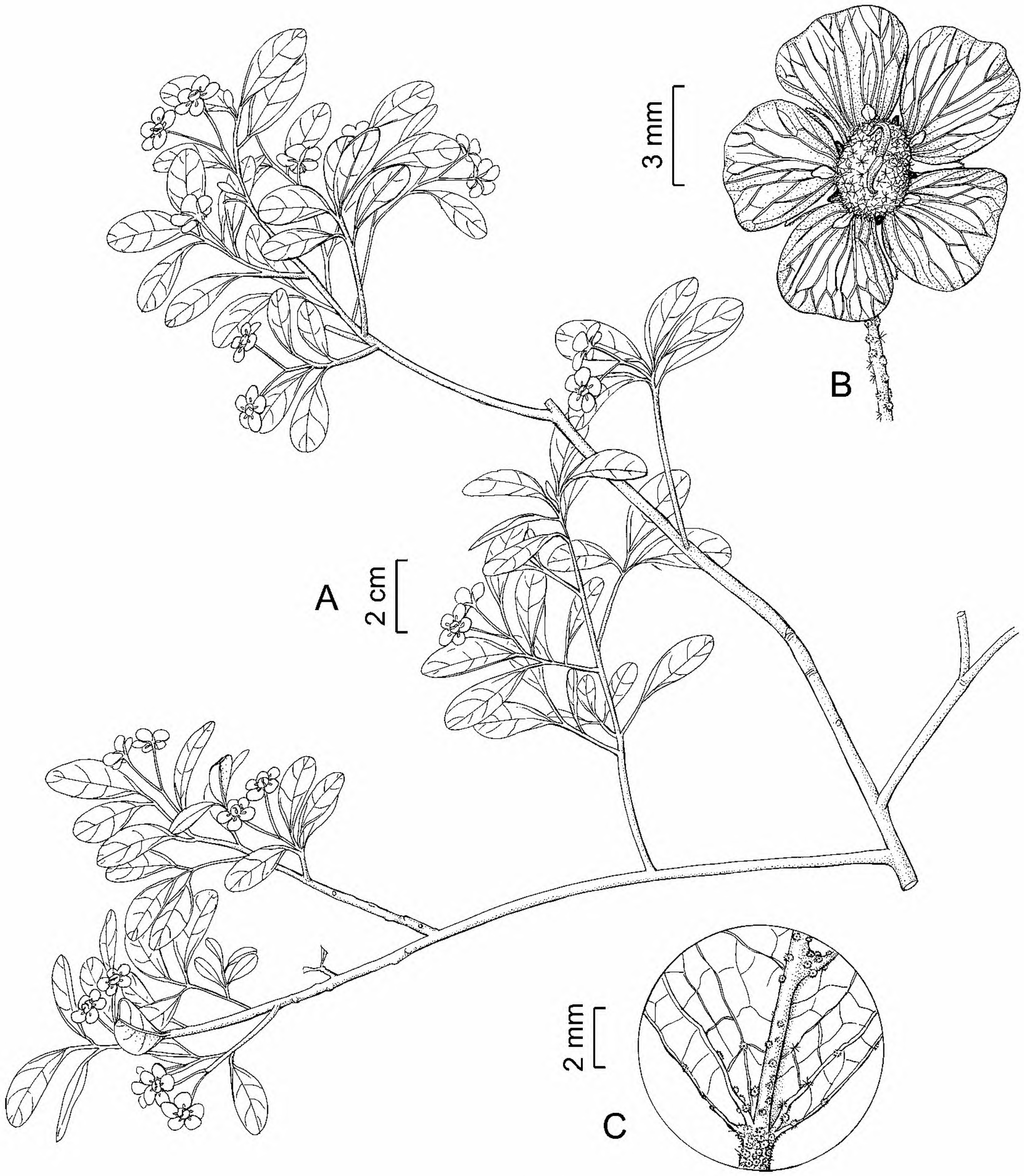


Figure 2. *Dombeya milleri* Appleq. & Bosser. —A. Habit. —B. Flower. —C. Domatia. A–C from *Miller et al. 10695* (MO).

Etymology. *Dombeya milleri* is named in honor of James S. Miller (MO, 1953–), an expert on the flora of Madagascar and primary collector of the selected type specimen. Jean Bosser (P) first identified this as a new species and hence shares authorship of the name.

Paratypes. MADAGASCAR. **Antsiranana:** DIANA, Montagne des Français, 12°19′22″S, 049°20′11″E, 178 m, 9 Dec. 2006 (fl.), *T. Andriamihajarivo et al. 1056* (MO); Montagne des Français, 12°19′28″S, 049°20′14″E, 290 m, 19 Jan. 2003 (fl.), *J. S. Miller*, *W. L. Applequist*, *J. Rabenantoandro & R. Ranaivojaona 10704* (MO); DIANA, Montagne des Français, 12°22′44″S, 049°21′57″E, 335 m, 25 Feb. 2007 (fr.), *L. J. Razafitsalama 1199* (MO, US); Montagne des Français, 28 Feb. 1964 (fl.), *Service Forestier 23242* (P [4]).

17. Dombeya ratovosonii Appleq. & Bosser, sp. nov. TYPE: Madagascar. Antsiranana: DIANA region, Montagne des Français, forêt d'Antaola-

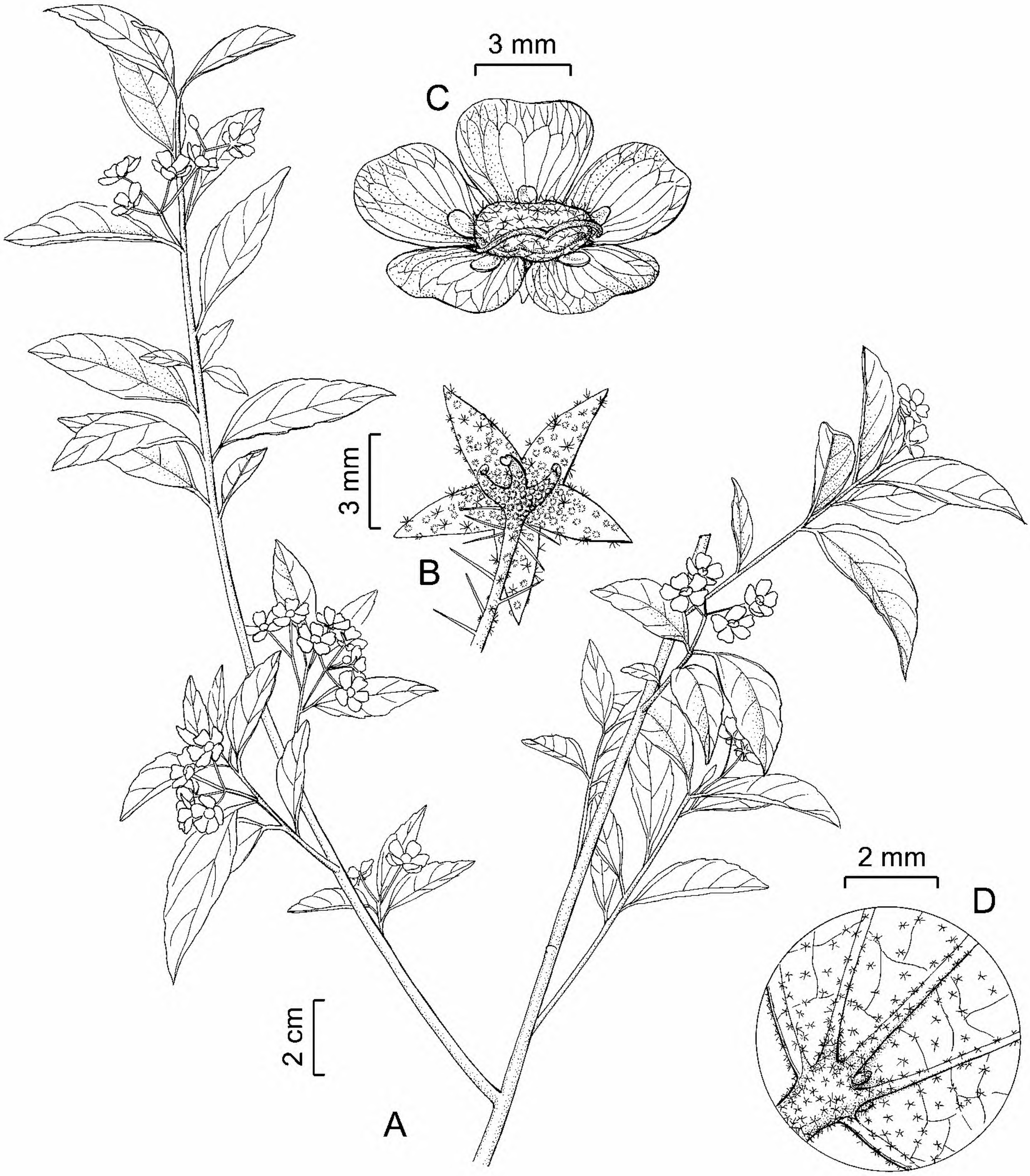


Figure 3. *Dombeya ratovosonii* Appleq. & Bosser. —A. Habit. —B. Calyx with bracteoles. —C. Flower. —D. Domatia. A–D from *Ratovoson et al. 1265* (MO).

naomby, forêt sèche, 12°22′25″S, 049°21′11″E, 385 m, 22 Mar. 2007 (fl.), *F. Ratovoson 1265* (holotype, MO!; isotypes, Centre National d'Application des Recherches Pharmaceutiques, not seen, P not seen, TAN not seen, US!). Figure 3.

Diagnosis. Distinguished from *Dombeya gautieri* Dorr & Skema by narrowly elliptical to oblong-elliptical or lanceolate unlobed leaves, staminodes narrower, corona and filaments shorter and hidden by ovary, ovary stellate. Distinguished from *D. milleri* Appleq. & Bosser by somewhat larger, narrowly elliptical to oblong-elliptical or lanceolate leaves, with acute apices and semicraspedodromous (vs. reticulodromous) secondary venation; indument of petioles, leaves, and inflorescences stellate (vs. long-fimbriate lepidote to flattened semi-stellate).

Shrub to 6 m or small tree; twigs pale brown, the youngest stellate and/or with scurfy indument;

stipules caducous, lanceolate to subulate, 3–5.5 mm, sparsely stellate; stipule scars on young twigs irregularly hemielliptical, pale, the distal margin slightly prominent. Leaves narrowly elliptical to lanceolate, oblong-lanceolate, or oblong-elliptical, 4–10.5 × 1.5–3.5 cm; petiole 4–10 mm, stellate; base rounded, occasionally slightly oblique; apex acute, often with a rounded tip; margins subentire to crenulate, with glands in rounded protrusions; both surfaces sparsely stellate; basal veins 3 to 5, if 5 the outer weak; main secondary veins above base 4 or 5 per side, visible but inconspicuous on adaxial surface, tertiary veins between midrib and long inner basal veins sometimes subscalariform; roofed domatia usually present in axils of basal veins with midrib, sometimes with a large swollen roof and very small opening, and small domatia often present in axils of secondary veins. Inflorescences 1(2) per node, 2- to 9-flowered; sometimes with 2 bracteoles subtending the group of pedicels; peduncle 1–13.5 mm; pedicels 6.5–13 mm, often curved shortly below flower, shorter or longer than peduncle; peduncle and pedicel stellate; bracteoles usually persistent, 0.7–1.6 mm, lanceolate to deltoid, sparsely stellate, borne immediately beneath flower. Sepals not reflexed, 2.4–3.3 mm, stellate; petals white, 4.5–5.4 × 4.5–5.5 mm, broadly obovate, slightly asymmetrical, generally pressing open flat and possibly rotate in living material post-anthesis; corona highly reduced (0.2 mm), flattened and hidden beneath ovary; stamens 5, alternating with petals; filaments 0.2 mm, hidden by ovary; anthers 0.4–0.5 mm, deltoid; staminodes oppositipetalous, spatulate, 1.4–2.2 mm; styles 2, divided to ovary, 1.7–2.8 mm; ovary stellate, at anthesis very flat. Immature fruit somewhat 2-lobed, to 2.8 × 2 mm, vertically somewhat compressed, stellate, with considerable empty space inside locules while developing ovules are still small; ovules 2 per locule, not at all winged; possibly only 1 seed maturing, immature seeds irregularly ellipsoid, to 1.4 mm; no mature seeds seen.

Distribution, habitat, and phenology. *Dombeya ratovosonii* is native to deciduous forests in extreme northern Madagascar; it has been reported on sand from elevations of 200 and 385 m. It flowers in February and March; immature fruits have been collected in March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ratovosonii* is noted as Vulnerable or VU, D; two locations relatively close together are known, one of which is in good condition and is to be protected in the future.

Discussion. *Dombeya ratovosonii* shares the extreme floral morphology of *D. milleri*; the two are presumed to be sister species. Leaves of *D. ratovosonii* are lanceolate to elliptic-oblong with more or less acute apices, whereas those of *D. milleri* are obovate with a rounded apex and somewhat smaller so far as is known from the very limited material. Leaves of *D. ratovosonii* have semicraspedodromous venation, as is usual in this section, whereas those of *D. milleri* are reticulodromous. The indument of the petioles, leaves, and inflorescences is stellate in *D. ratovosonii* versus fimbriate-lepidote or semi-stellate in *D. milleri*. Given the near certainty that the two are closely related, this provides yet another piece of evidence that the structure of the trichome or scale is quite labile in *Dombeya*.

Etymology. *Dombeya ratovosonii* is named in honor of Fidy Ratovoson (MO, 1972–), a Malagasy botanist and collector of the selected type specimen. Jean Bosser (P) first identified this as a new species and hence shares authorship of the name.

Paratypes. MADAGASCAR. **Antsiranana:** Sahafary, S of Diego [Suarez], Mar. 1962 (fr.), *M. Keraudren 1675* (P [3]); Sahafary, basin of the Saharaina, 200 m, 20 Feb. 1962 (fl.), *Service Forestier 20988* (P [4]).

V. Dombeya ser. **Selinala** Arènes, Candollea 16: 362. 1958. TYPE: *Dombeya selinala* Arènes.

Dombeya subser. *Digynae* Arènes, Candollea 16: 368. 1958. TYPE: *Dombeya digyna* Hochr.

Dombeya subser. *Mafimafy* Arènes, Candollea 16: 382. 1958. TYPE: *Dombeya mafimafy* Arènes [= *D. subviscosa* Hochr.].

Dombeya subser. *Sely* Arènes, Candollea 16: 379. 1958. TYPE: *Dombeya sely* Arènes.

Dombeya ser. *Valafotsy* Arènes, Candollea 16: 379. 1958. TYPE: *Dombeya valafotsy* Arènes [= *D. selinala* Arènes].

Young twigs stellate, papillate, small-scaled or glabrous; stipule scars usually narrow, dark, not prominently elevated or conspicuous (in one species, *Dombeya digyna*, small but broad, dark, slightly prominent). Leaves lanceolate to ovate (elliptical, oblong-elliptical, oblanceolate); basal veins (3 to)5 (to 7); secondary veins 3 to 10(to 12); domatia present or absent, basal and sometimes in axils of secondary veins; petioles stellate, papillate, or glabrous. Inflorescences umbellate (umbelliform cymes, or in *D. parvipetala*, few-flowered, mostly dichotomously branching cymes), stellate, papillate, glabrous, or small-scaled; peduncles 0.5–13(–22) mm, usually shorter than pedicels. Petals elliptical to obovate, symmetrical (to slightly asymmetrical), mostly convex at (or after) anthesis; stamens (10 to)15; staminodes

± oppositisepalous, shorter than or equal to (longer than) longest fertile filaments; ovary papillate or stellate, rarely glabrous.

Distribution and habitat. *Dombeya* ser. *Selinala* is widely distributed in dry forests and bush in northern, western, and southern Madagascar, at altitudes from sea level to 1200 m; one rare species (*D. micrantha* Appleq.) is recognized from humid eastern forest.

Discussion. *Dombeya* ser. *Selinala* is a relatively cohesive group of 13 species, almost all from dry habitats, that is characterized by small flowers with symmetrical or slightly asymmetrical petals that mostly become at least somewhat concave at (or after in *D. tulearensis* Arènes) anthesis. By contrast, species in other series have usually asymmetrical, never concave petals, as is observed also to be the norm for *Dombeya* subg. *Xeropetalum*. The leaves in *Dombeya* ser. *Selinala* are often lanceolate to ovate and frequently have domatia and/or a papillate indument. In all but one species (*D. parvipetala*), the sepals are usually or always reflexed post-anthesis. Over half of the included species have staminodes shorter than, or similar in length to, the longest filaments, whereas in all other series, the staminodes are almost always longer than the filaments. *Dombeya* ser. *Selinala* is suggested to represent a monophyletic group.

Dombeya parvipetala, formerly included in *Dombeya* sect. *Xeropetalum* because of its cymose inflorescences, is herein considered to belong within *Dombeya* sect. *Decastemon*. Its few-flowered, delicate inflorescences are dichotomously branching, whereas those of all other species of *Dombeya* sect. *Xeropetalum* are usually at least somewhat asymmetrical. The cymose condition here may be a reversal from an umbellate ancestral state, the capacity for which is demonstrated by aberrant short-cymose inflorescences in a number of other species. In other characters, such as near-symmetrical petals, narrowly lanceolate, papillate leaves, and xerophytic habitat preference, this species bears an obvious resemblance to the core group of *Dombeya* ser. *Selinala*.

KEY TO THE SPECIES OF *DOMBEYA* SER. *SELINALA*

1a. Inflorescence a slender, small but well-developed, mostly dichotomizing (or trichotomizing) cyme ..... 24. *D. parvipetala*

1b. Inflorescence an umbel or umbelliform cyme.

2a. Ovary papillate to glabrous.

3a. Young twigs, leaves, and petioles stellate, with trichomes at least partly reddish in color..... 29. *D. tulearensis*

3b. Young twigs, leaves, and petioles papillate to glabrous or whitish stellate or scaly.

4a. Staminodes shorter than longest filaments of fertile stamens.

5a. Leaves lanceolate, occasionally to narrowly ovate; bracteole scars at anthesis well below flower, usually near the midpoint of pedicel; petals narrowly obovate, 1.9–2.5 mm broad; ovary papillate at anthesis; Montagne des Français ..... 19. *D. ambohitrensis* Arènes

5b. Leaves lanceolate to ovate, elliptical, oblong, or narrowly lanceolate (rarely to oblong-oblanceolate or aberrantly obovate); bracteole scars at anthesis from immediately below flower to moderately lower (very rarely near midpoint of pedicel); petals obovate to elliptical, (2–)2.4–3(–5) mm broad; ovary, when papillate, usually with a few trichomes at apex and on base of style at anthesis; northwestern to southwestern Madagascar ..... 28. *D. subviscosa*

4b. Staminodes equal to or longer than longest filaments of fertile stamens.

6a. Domatia absent at base, present in axils of secondary veins and sometimes the largest tertiary veins arising from lateral basal veins; petals on type specimen < 4.5 mm; stamens 10; humid forest of eastern Madagascar ..... 23. *D. micrantha*

6b. Domatia absent or seldom present in axils of basal and secondary veins; petals normally > 4.5 mm; stamens 15; northwestern to southeastern Madagascar.

7a. Domatia present in axils of basal and secondary veins; pedicels < 10 mm, reddish papillate and ± stellate ..... 27. *D. sely*

7b. Domatia absent; pedicels > (8–)10 mm, glabrous to sparsely stellate.

8a. Bracteole scars at anthesis well below flower, with pedicel sometimes thickened above; petals without a red basal spot; calyx lacking a conspicuous basal cup, the upper portions of the sepals persistent; southeastern Madagascar .... 26. *D. selinala*

8b. Bracteole scars at anthesis immediately or closely below flower; petals often with a dark red basal spot; calyx with an unusually well-developed basal cup, the free portions of the sepals caducous in fruit; southwestern to northwestern Madagascar.

9a. Petioles stellate; leaves lanceolate to ovate, occasionally elliptical, some rarely to oblong-oblanceolate to obovate, (1.2–)1.8–3.6(–4.3) cm broad; margins usually crenulate-serrulate to serrulate with numerous small teeth, rarely crenate-serrate; bracteoles with ciliate margins ..... 18. *D. ambalabeensis* Arènes

9b. Petioles glabrous; leaves narrowly lanceolate to lanceolate, rarely to ovate, 1–2.4(–3) cm broad; margins usually with relatively few shallow teeth with a long forward-pointing basal margin; bracteoles with papillate margins..... ..... 20. *D. anakaensis* Arènes

2b. Ovary at least partly stellate.

10a. Young twigs papillate, bearing small irregular flattened scales, or glabrous.

11a. Leaves usually asymmetrical at the base, domatia absent; bracteole scars immediately below flower at anthesis; stamens 10; southwestern Madagascar around Ambovombe ..... 21. *D. danguyi*

11b. Leaves with the base occasionally oblique but not otherwise strongly asymmetrical, domatia present or absent; bracteole scars variably positioned, well below flower if leaves are narrowly lanceolate; stamens 15; southwestern to northern Madagascar.

12a. Leaf margins variably toothed, seldom crenulate-sinuate, not strongly sinuate; sepals mostly to entirely reflexed at least post-anthesis; staminodes shorter than longest filaments; northwestern to southwestern Madagascar ..... 28. *D. subviscosa*

12b. Leaf margins irregularly sinuate to crenate-sinuate; sepals mostly not reflexed; staminodes about equal to longest filaments; extreme northern Madagascar ..... 30. *D. vohemarensis*

10b. Young twigs at least sparsely stellate.

13a. Petals strongly reflexed ..... 25. *D. sakamaliensis* Appleq.

13b. Petals never strongly or consistently reflexed.

14a. Calyx stellate ..... 22. *D. digyna* Arènes

14b. Calyx glabrous (rarely with aberrant stellate patches on some flowers) or papillate.

15a. Domatia usually present at base and/or in axils of secondary veins of larger leaves; inflorescences (1- to)2- to 15(to 22)-flowered; pedicels papillate (rarely stellate); staminodes shorter than filaments of longest fertile stamens ..... 28. *D. subviscosa*

15b. Domatia absent; inflorescences 1- to 7(8)-flowered; pedicels stellate or glabrous (seldom papillate); staminodes at least slightly longer than filaments of longest fertile stamens.

16a. Bracteole scars at anthesis well below receptacle, with pedicel sometimes thickened above; petals without a red basal spot; calyx lacking a conspicuous basal cup, the upper portions of the sepals persistent; southeastern Madagascar ..... 26. *D. selinala*

16b. Bracteole scars at anthesis immediately or close below receptacle; petals often with a dark red basal spot; calyx with an unusually well-developed basal cup, the free portions of the sepals caducous in fruit; southwestern to northwestern Madagascar ..... 18. *D. ambalabeensis*

18. Dombeya ambalabeensis Arènes, Candollea 16: 389. 1958. TYPE: Madagascar. Fianarantsoa: bassin de la Malio (affluent de Mangoky) près d'Ambalabe, restes de forêt tropophile et bush xerophile, sur sables siliceux et grès, 400–450 m, 23–27 Nov. 1946 (fl.), *H. Humbert 19461* (holotype, P!; isotype, MO!).

Tree to 10–12(–20) m or shrub to 3 m; twigs dark brown, the youngest stellate to sparsely stellate with small white trichomes; stipules caducous, lanceolate, 1.4–2.5 mm, stellate; stipule scars on young twigs narrow but often relatively large and conspicuous. Leaves usually lanceolate to ovate (especially when young), occasionally elliptical, or rarely oblong-oblanceolate to obovate, (3.5–)5–9.5(–11.7) × (1.2–)1.8–3.6(–4.3) cm; petiole (2–)4–10(–12) mm, stellate; base ± rounded, occasionally tending toward cuneate, truncate, or very slightly cordate; apex acuminate, the immediate tip often rounded, or rarely acute; margins irregularly crenulate-serrulate to serrulate or rarely crenate-serrate, usually with many small teeth per side, rarely with few and/or larger teeth, with glands inconspicuous, located in tooth apices, or absent; both surfaces sparsely stellate, often bearing tiny flat papillae; basal veins 5 to 7(8), all but the inner pair weak; main secondary veins above base 5 to 10 per side with smaller similar veins often interspersed, visible on adaxial surface; domatia absent. Inflorescences 2- to 7-flowered, sometimes numerous and forming relatively large clusters; peduncle 2–6.5 mm, stellate or rarely glabrous, occasionally paired in leaf axils or thick and flattened in a large inflorescence and giving the appearance of 2 fused peduncles; pedicels (12–)16–25(–33) mm, glabrate with rare stellate trichomes or stellate patches in aberrant individual flowers; bracteoles rapidly caducous, lanceolate to ovate, oblong, or elliptical, 0.8–1.2 mm, with long-ciliate margins, the bracteole scars at flowering directly under receptacle or close to it. Sepals fused into unusually well-developed cup at base, the free portions 3–3.8 mm, reflexed with a gradual curve, with large, conspicuous glandular patches, caducous in fruit and the basal cup remaining and prominently visible, glabrous with rare stellate patches as an aberration in individual flowers; petals white, sometimes with a dark red basal mark, or pale yellow, (4.6–)6–7.5(–8) × (2–)2.6–4(–5) mm, elliptical to obovate, slightly asymmetrical, mostly concave; corona dark red, 1–1.7 mm; stamens 15; filaments 0.7–2.5 mm; anthers yellow,

0.8–1.1(–1.5) mm; staminodes narrowly spatulate, 2.4–3.3 mm; style white, 2.5–4 mm; style branches 2, white, 0.5–0.8 mm; ovary glabrous or papillate (apically stellate). Fruit subglobose with a narrowed apex where style base persists at least through most of development, 3–4(–4.5) mm diam. at maturity, dark, glabrous to sparsely papillate or rarely sparsely stellate at apex; seeds 2 per fruit, dark brown, broadly ellipsoid to broadly oblong-ellipsoid, at full maturity plump with one flattened side, 2.5–2.7 mm, otherwise irregularly wrinkled and shrunken, with a minutely ridged surface.

Discussion. *Dombeya ambalabeensis* has an unusual calyx morphology that is shared with only one other recognized species, *D. anakaensis*. In both taxa, the free portion of the sepal is caducous in fruit, leaving the cup of the calyx at the base of the nearly globose fruit, which retains the spreading petals. There is also a specimen from Imanombo (*Service Forestier 22510*) with similar calyx morphology that remains incertae sedis but might represent a third, herein undescribed species related to these two.

Three subspecies are recognized within *Dombeya ambalabeensis*, one of which was formerly recognized at the species level as *D. analavelonae* Arènes. *Dombeya ambalabeensis* and *D. analavelonae* have equal priority; the former is preferred because it pertains to the widespread subspecies and has been utilized far more often in the herbarium.

One specimen can be placed within *Dombeya ambalabeensis*, but not within any recognized subspecies: *Morat 4727* was collected from dry forest in northwestern Madagascar. It has very long pedicels (3.4–4.5 cm), large flowers (petals to 9 mm), and broad-based leaves with crenate-serrulate margins; the ovary is finely stellate apically. Unfortunately, it is past anthesis, and the androecia have been lost. Although this specimen was collected closest to the type locality of the poorly known *D. ambalabeensis* subsp. *ambongensis* Arènes, its morphology is entirely inconsistent with that taxon. It more closely resembles the southwestern *D. ambalabeensis* subsp. *analavelonae* (Arènes) Appleq., from which it is distinguished by its inflorescence and flower size and different ecological preferences. Placement within *D. ambalabeensis* subsp. *analavelonae* would risk obscuring the existence of a genetically distinctive northwestern subspecies; however, formal description of this population as a subspecies based on a single specimen might lead to excessive proliferation of names. Further collections of this population (if it still exists) would be highly desirable.

Specimen incertae sedis. Madagascar. **Mahajanga:** forêt de Kassife, Causse du Kelifely, forêt tropophile sur calcaire, Nov. 1974 (fr.), *Morat 4727* (MO [2]).

KEY TO THE SUBSPECIES OF *DOMBEYA AMBALABEENSIS*

1a. Ovary apically pubescent; Analavelona..... ..... 18c. subsp. *analavelonae*
1b. Ovary glabrous to papillate.
  2a. Inflorescences 2- to 7-flowered; pedicels 20–30 mm; stamens 15; staminodes 2.4–3.3 mm; ovary glabrous to papillate; southern and southwestern Madagascar..... ..... 18a. subsp. *ambalabeensis*
  2b. Inflorescences 1- or 2-flowered; pedicels 10–18 mm; stamens 10(to 15); staminodes 1.8–2 mm; ovary glabrous; northwestern Madagascar (Namoroka) .... 18b. subsp. *ambongensis*

18a. Dombeya ambalabeensis Arènes subsp. **ambalabeensis.**

Inflorescences 2- to 7-flowered; bracteole scars usually close to receptacle; pedicels 20–30 mm; petals (4.6–)6–7.5(–8) mm; stamens 15; staminodes 2.4–3.3 mm; ovary glabrous to papillate.

Distribution, habitat, and phenology. *Dombeya ambalabeensis* subsp. *ambalabeensis* is native to dry and riverine forests of southern and southwestern Madagascar; it is found on both sand and limestone at altitudes of 130–850 m. It flowers from October to December and fruits from January to May.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ambalabeensis* subsp. *ambalabeensis* is noted as Least Concern or LC.

Vernacular names. Selinaomby (*Service Forestier 3391*), valo (*Service Forestier 4135*, *4986*), valosely (*Service Forestier 4648*).

Discussion. Leaves of *Dombeya ambalabeensis* subsp. *ambalabeensis* are reportedly caducous (*Perrier de la Bâthie 16656*) and glossy when young with veins prominent on both surfaces (*Phillipson 2499*); in dried material, the veins are not prominent.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** "bassin de la Malio (affluent de Mangoky), près d'Ambalabe," *Humbert 19338* (P), *19360* (P); Isalo, *Keraudren 1098* (P); pk. 40, route Ihosy–Ivohibe, *Peltier & Peltier 5535* (P [2]); Ambinda, *Peltier & Peltier 5768* (P [2]); Ranohira, Ihosy, *Reserves Naturelles 10692* (P); 10 km NE of Ihosy, *Service Forestier 29067* (P [2]). **Toliara:** Ankazoabo, *Bosser 17232* (P); Zambomakondro, Sakaraha, *Decary 18924* (P); s. loc., *Homolle 1434* (MO, P [2]); Zombitsy (Sakaraha), *Humbert 29650* (P); Zombitsy, *Morat 3478* (MO, P [2]); vallée de Fiherenana, *Perrier de la Bâthie 16656* (MO, P [2]); Beza Mahafaly Reserve, parcelle 1, *Phillipson*

1726 (MO, P); Beza Mahafaly Reserve, valley of Ambinda stream, *Phillipson 2488* (MO, P); Beza Mahafaly Reserve, parcelle 1, *Phillipson 2499* (MO, P); Morafeno, Ampanihimahasoa, 12 km SE of Ankazoabo, *Randrianaivo et al. 1061* (MO, P); Hazoroa, Tulear, *Service Forestier 3391* (P); Imonty, Ankazoabe, *Service Forestier 4135* (P [2]); Anketa, Tulear, *Service Forestier 4648* (P); Hazoroa, Sakaraha, *Service Forestier 4986* (P); Beza, Bekily, *Service Forestier 11160* (MO, P [2]); Lac Ihotry [Iotry], *Service Forestier 20711* (P); Beza Mahafaly Reserve, parcelle 1, *Sussman 386* (MO); Zombitsy forest, 11 km E of Sakaraha, *Willing 35* (MO).

18b. Dombeya ambalabeensis Arènes subsp. **ambongensis** Arènes, Candollea 16: 390. 1958. TYPE: Madagascar. Mahajanga: tsingy de Namoroko (Ambongo), 1926 (fl.), [*G.*] *Petit s.n.* (holotype, P!).

Inflorescences 1- or 2-flowered; bracteole scars slightly below flower; pedicels 10–18 mm; petals 6 mm; stamens 10(to 15); staminodes 1.8–2 mm; ovary glabrous.

Distribution, habitat, and phenology. *Dombeya ambalabeensis* subsp. *ambongensis* is known only from Namoroko in northwestern Madagascar, on tsingy (limestone karst).

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ambalabeensis* subsp. *ambongensis* is noted as Vulnerable or VU, D. Though the only known locality is protected, the fact that this plant has not been re-collected since 1926 despite many later collections made in the area suggests that the population is very small. Efforts to relocate this taxon, which may be very rare, would be desirable.

Discussion. The holotype of *Dombeya ambalabeensis* subsp. *ambongensis* was collected far outside the otherwise known range of *D. ambalabeensis*. It is, unfortunately, in poor condition, with few flowers, and the leaves are clearly immature (2–4 cm long, with 2–3 mm petioles and poorly developed venation) and severely damaged. It is distinguished from *D. ambalabeensis* subsp. *ambalabeensis* by having fewer flowers per inflorescence, smaller inflorescences, shorter staminodes, and possibly fewer stamens.

18c. Dombeya ambalabeensis Arènes subsp. **analavelonae** (Arènes) Appleq., comb. et stat. nov. Basionym: *Dombeya analavelonae* Arènes, Candollea 16: 372–373. 1958. TYPE: Madagascar. Toliara: forêt d'Analavelona (bassin du Fiherenana), forêt tropophile sur basalte, 1000–1200 m, 15–19 Dec. 1946 (post-fl.), *H. Humbert 19757* (holotype, P!; isotype, P!).

Inflorescences 2- to 5-flowered; bracteole scars from slightly below flower to immediately beneath receptacle, often separated; pedicels 20–30 mm; petals 6 mm; stamens 15; staminodes 3 mm; ovary stellate on apical portion.

Distribution, habitat, and phenology. *Dombeya ambalabeensis* subsp. *analavelonae* is endemic to Analavelona in southwestern Madagascar, on basalt at over 1000 m elevation. The massif of Analavelona has a semi-humid forest type that occurs nowhere else in the region. The type was past flowering when collected in December.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ambalabeensis* subsp. *analavelonae* is noted as Vulnerable or VU, D. Only one population is known, and it is probably endemic to the massif of Analavelona, as no other similar habitat exists in the region. This locality is subject to less anthropogenic damage than most formally unprotected forests because of its cultural significance. However, since recent collectors have not relocated this taxon, its population is likely to be small.

Vernacular name. Selinala (in Bara dialect; *Humbert 19757*).

Discussion. The sole specimen of *Dombeya ambalabeensis* subsp. *analavelonae* known from Analavelona is distinguishable from *D. ambalabeensis* subsp. *ambalabeensis* by the sparse stellate pubescence on the immature fruit. The basal veins may be consistently more than five, and the marginal teeth of this specimen are somewhat more irregular than usual; it is otherwise unremarkable. As the massif of Analavelona represents a different habitat, with a subhumid forest that is unique in the region, this population may well be genetically distinctive.

19. Dombeya ambohitrensis Arènes, Candollea 16: 385. 1958. TYPE: Madagascar. Antsiranana: Montagne des Français, Diégo-Suarez, 24 Mar. 1955 (fl.), *Service Forestier 13137* (holotype, P!; isotypes, P [2]!, TEF not seen, TEF image!).

Tree to 9 m, DBH 13 cm; twigs dark brown, the youngest sparsely stellate with tiny trichomes or scurfy scales or papillate; stipules caducous, almost never present, deltoid, 0.5 mm, scaly or papillate; stipule scars on young twigs narrow, inconspicuous. Leaves lanceolate, occasionally to narrowly ovate, 5–9 × 1.8–3(–4) cm; petiole (4–)6–9(–10) mm, bearing small flat papillae and occasionally stellate trichomes; base rounded to oblique; apex acuminate;

margins irregularly crenate-serrulate to crenulate, with glands variably located in apices or apical margins of teeth or between teeth, occasionally protruding near apex; both surfaces papillate with tiny flat papillae or occasionally glabrate, at least sometimes stellate when young and sparse stellate indument sometimes persisting at maturity, occasionally also sparsely pilose mostly around midrib beneath; basal veins 5(to 7), the outer weak; main secondary veins above base (4)5 or 6(7) per side, visible on adaxial surface; domatia present or absent at base, if present small but often well developed, surrounded by unbranched trichomes. Inflorescences usually at least 2 per node, (3- to)6- to 10(to 14)-flowered, the largest usually umbelliform cymes with 2(3) short branches; peduncle 1.5–6 mm, papillate; pedicels 8–12(–16) mm, papillate; bracteoles very early caducous, 1 mm, ovate, papillate, at full elongation of pedicel bracteole scars well below flower, usually near the midpoint of pedicel. Sepals white, 2.4–3.8 mm, reflexed, papillate; petals white, 4–7 × 1.9–2.5 mm, narrowly obovate, mostly concave, symmetrical or nearly so; corona 0.5 mm; stamens 15; filaments 1.4–3.5(–5) mm; anthers 0.7–1.1 mm; staminodes linear to narrowly spatulate, 1.5–2.2 mm, always shorter than longest filaments; style 1.6–2.4 mm, basally glabrous; style branches two, 1–2 mm; ovary papillate. Fruit subglobose, blackish when dried, probably green in living material, 3–3.4 mm diam. at maturity, papillate; seeds 2 per fruit, possibly sometimes only 1 maturing, pale brown, broadly ellipsoid, to at least 2.3 mm, with 1 concave flattened side, surface papillate at one end and finely striated; mature seeds probably not seen.

Distribution, habitat, and phenology. *Dombeya ambohitrensis* is endemic to Montagne des Français in extreme northern Madagascar. It occurs in dry deciduous forest, at least sometimes on tsingy; the only reported altitude is 325 m. It flowers in March; fruits have been collected in May.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya ambohitrensis* is noted as Vulnerable or VU, D. This species is known to exist only at one locality, but that locality is in relatively good condition and is soon to be formally protected. The species is described as "occasional" in that area (*Razafitsalama et al. 579*), implying that the population may not be large.

Vernacular name. Sely (*Service Forestier 13137*).

Discussion. *Dombeya ambohitrensis* bears obvious affinities to the *D. subviscosa* complex. It is distinguished from *D. subviscosa* primarily by its narrower petals and papillate ovary and fruit; the ovary of *D. subviscosa* subsp. *subviscosa* is often glabrate or rarely papillate at anthesis but becomes stellate post-anthesis. The leaves of *D. ambohitrensis* are commonly lanceolate, giving it a particular resemblance to the narrow-leaved southwestern *D. subviscosa* subsp. *sakarahae* (Arènes) Appleq., but its leaf margins are usually crenate-serrulate to crenulate, whereas those of *D. subviscosa* subsp. *sakarahae* are quite variable but seldom crenulate.

Ramananjanahary et al. 27, a tree to 12 m and 20 cm DBH that is largely glabrous and lacking domatia, has relatively large fruits and flowers. The leaves sometimes have unusually long petioles, and the inflorescences are few-flowered. This might be a hybrid between *Dombeya ambohitrensis* and *D. vohemarensis*, which has, however, never been collected from Montagne des Français.

Additional specimens examined. MADAGASCAR. **Antsiranana:** Montagne des Français, *Keraudren 1613* (MO [2], P [2]), *1619* (P), *1628* (P); Montagne des Français, 5 km NE of Andranomanitra, *Razafitsalama et al. 579* (MO, P); Montagne des Français, Joffreville, *Service Forestier 3558* (P [3]).

Possible hybrid specimen. MADAGASCAR. **Antsiranana:** Andranomanitra, Montagne des Français, *Ramananjanahary et al. 27* (MO, P).

20. Dombeya anakaensis Arènes, Candollea 16: 386–387. 1958. TYPE: Madagascar. Toliara: entre Anakao et Betioky, 25 Oct. 1940 (fl.), *R. Decary 16095* (holotype, P!; isotypes, P!, TAN not seen, TAN image!).

Dombeya anakaensis subsp. *multiflora* Arènes, Candollea 16: 387. 1958, syn. nov. TYPE: Madagascar. Toliara: Vineta, Tuléar, 20 Dec. 1955 (fl.), *Service Forestier 15598* (holotype, P!; isotypes, P!, TAN not seen, TAN image!).

Shrub to 4 m or small tree to 5 m, 10 cm DBH; twigs dark brown, glabrous except for occasional small stellate patches around nodes (where buds are normally stellate); stipules caducous, lanceolate, 1.5–2.7 mm, glabrous or glabrate; stipule scars on young twigs narrow but often pale, relatively conspicuous and prominent. Leaves narrowly lanceolate to lanceolate, very rarely to ovate, 4–9.5 × 1–2.4(–3) cm; petiole 5–10(–13) mm, glabrous; base rounded to slightly cordate; apex acuminate or narrowly acute; margins irregularly crenulate-serrulate to serrulate, the teeth shallow with a long forward-pointing basal margin and short apical margin, with yellowish glands usually located in apices of teeth; young leaves papillate and sometimes

sparsely stellate, at maturity both surfaces glabrous or glabrate with minute flat papillae and rare stellate trichomes; basal veins 5(to 7), all but the inner pair weak; main secondary veins above base 3 to 6(to 9) per side with smaller similar veins sometimes interspersed, visible but inconspicuous on adaxial surface; domatia absent. Inflorescences 2- to 7-flowered, sometimes numerous and forming relatively large clusters; peduncle (0.5–)2–7.5 mm, glabrous, occasionally partly divided making the inflorescence an umbelliform cyme; pedicels (8–)10–20(–36) mm, glabrate; bracteoles rapidly caducous, irregularly oblong to lanceolate, 1–1.2 mm, with papillate margins, scars borne immediately beneath flower (or slightly lowered). Sepals basally fused, the free portions (2–)3.3–3.8(–4.2) mm, almost always reflexed and sometimes displaying relatively large and conspicuous glandular patches, caducous in fruit and the basal cup remaining, glabrous with rare stellate patches as an aberration in individual flowers; petals white with a dark red basal mark, (4.3–)4.8–6.4(–7.6) × (2–)2.7–3.7(–4.3) mm, elliptical to obovate, slightly asymmetrical, mostly concave; corona (1–)1.3–2(–2.6) mm; stamens 15; filaments 0.5–2.4(–3) mm; anthers 0.7–1.2 mm; staminodes narrowly spatulate to linear, (1.5–)2.2–3 mm; style (2.6–)3.3–5.6 mm; style branches two, 0.6–0.8(–1) mm; ovary papillate. Fruit subglobose, often with a persistent style base, 3.5–4 mm diam. at maturity, dark, inconspicuously papillate; seeds 1 or 2 per fruit, dark brown, 2–2.6 mm, if 1 then irregularly shaped and not compressed, if 2 then broadly obovoid with 1 concave flattened side, nearly hemispherical, surface slightly papillate or minutely ridged.

Distribution, habitat, and phenology. *Dombeya anakaensis* is native to dry forest and bush of southwestern Madagascar, ranging as far north as Morondava on the western coast; it is reported on limestone, including tsingy, and red soil at altitudes of 30–350 m. It flowers from October to March and fruits from February to March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya anakaensis* is noted as Least Concern or LC.

Vernacular names. Ampelambatotse (*Service Forestier 15598*), satro (*Humbert 20192*), sely (*Rahantamalala 58*), valo (*Service Forestier 4516*).

Discussion. *Dombeya anakaensis* is clearly a close relative of *D. ambalabeensis*, with which it shares an unusual calyx morphology, particularly in fruit. *Dombeya anakaensis* can be distinguished by its often narrowly lanceolate leaves with more strongly serrulate, shallow but elongated teeth, and by the lack of stellate pubescence in the mature plant. The petals are on average slightly smaller, and the bracteoles have papillate rather than long-pubescent margins (however, as the bracteoles remain only on the tiniest buds, this character will seldom be available for observation). Existing collections describe *D. anakaensis* as a small tree or shrub, whereas *D. ambalabeensis* sometimes grows to large size (10–12 m, or in one report 20 m).

Leaves of *Dombeya anakaensis* are described as subcoriaceous (*Du Puy et al. MB622*). Two collections from Morondava (*Nicoll 165* and *Rahantamalala 58*), well north of the usual range, have very long pedicels and ovate or near-ovate leaves with very rounded, sometimes ill-defined teeth. However, their leaf morphology is not more extreme than that of two other specimens (mentioned below) from the Tulear region that are herein identified as *D. anakaensis*, and other characters are typical. Identity of this population may be questionable.

Two collections are believed to be hybrids of *Dombeya ambalabeensis* × *D. anakaensis*. *Chauvet 369* is glabrous but has very broad leaves with highly aberrant marginal teeth; *Phillipson & Rabesihanaka 3104* has narrow leaves but stellate pubescence especially on the leaves and petioles. Both come from a region where both putative parental species are to be found, and given the undoubted close relationship between the two species, cross-fertility would not be unlikely. A few other unusually broad-leaved but otherwise typical specimens are herein identified as *D. anakaensis*; in addition to the material from Morondova (above), two were collected along the road from Tulear to Sakaraha (*Service Forestier 511* and *20192*), again in the region of sympatry. It is tempting to identify these as possibly part of a hybrid zone as well; however, it is also possible that the limited available material of *D. anakaensis* does not adequately reflect the range of variation typical of mature leaves in this species.

Additional specimens examined. MADAGASCAR. **Toliara:** Atsimo-Andrefana, Belalanda, Ranobe, *Andrianjafy et al. 1689* (MO); Km. 25,500, rte. from Tuléar to Tana, *Chauvet 130* (MO, P); 45–55 km E of Tulear on rd. to Andranovory, *Croat 31073* (MO); Tanety Miary, *Dequaire 27507* (MO, P); ca. 50 km W of Ampanihy on rte. to Androka, NE of Vangiambato, *Du Puy et al. MB622* (MO, P); valley of the Onilahy near Tongobory, Ranomay, *Humbert 20192* (MO, P); plateau Mahafaly, 3 km from village of Beomby (W of Edjeda), *Keraudren 815* (P [2]); 53 km SW of Ampanihy, *Labat et al. 2089* (P); 45 km N of Morondava on Belo Tsiribihina rd., 20°03′S, 044°38′E, *Nicoll 165* (MO, P); Ambatoveve, Betioky, *Peltier & Peltier 1357* (MO, P); Morondava, *Rahantamalala 58* (P); Atsimo-

Andrefana, Belalanda, Ranobe, *Razafindraibe et al. 179* (MO); gorges of the Fiherenana, Tulear, *Service Forestier (Chauvet) 369* (MO [2]); rte. Tulear–Sakaraha (Km. 26), *Service Forestier 511* (P); Ambohimalaha, Velona, Tuléar, *Service Forestier 4516* (P); rte. Tuléar–Sakaraha, *Service Forestier 20192* (MO, P); N of Andranohinaly (PK 45, rte. Tuléar–Sakaraha), *Service Forestier 20762* (P).

Hybrid specimens. MADAGASCAR. **Toliara:** gorge of the Fiherenana, Tuléar, *Chauvet 369* (P [12]); valley of the Fiherenana, near Beantsy, *Phillipson & Rabesihanaka 3104* (MO, P).

21. Dombeya danguyi Hochr., Candollea 3: 39–40. 1926. TYPE: Madagascar. Toliara: distr. d'Ambovombe [Androy], sable [sand], 14 Apr. 1924 (fl.), *R. Decary 2632* (holotype, P!; isotypes, G not seen, G image!, MO!, P!).

Shrub or small tree; twigs dark to grayish brown, the youngest glabrous or bearing minute white scales or flattened papillae; stipules caducous, broadly deltoid, 0.5–1 mm, papillate; stipule scars on young twigs narrow, usually inconspicuous, occasionally pale and relatively conspicuous. Leaves narrowly lanceolate or occasionally lanceolate, 4.5–10 × 0.8–2.4 cm; petiole 5–14(–20) mm, papillate to glabrate; base moderately oblique to rounded, with basal insertion usually asymmetrical; apex narrowly acute, often asymmetrically, to acuminate; margins shallowly to conspicuously crenate-denticulate to crenate-dentate, crenate-serrulate, or shallowly wavy, with pale or brownish glands usually located in apical margin of teeth or in tooth apices; both surfaces usually at least sparsely papillate with small flat papillae, rarely glabrate, the upper surface grayish olive-green; basal veins (3 to)5(to 7), all but the innermost weak; main secondary veins above base 7 to 12 per side, usually visible on adaxial surface, often dark-colored; domatia absent. Inflorescences 1- to 4(5)-flowered, frequently an umbelliform cyme with ± divided peduncle; peduncle 1–6(–8) mm, papillate or bearing small white scales or rarely glabrous; pedicels (5–)10–20(–23) mm, at least sparsely papillate or scaly; bracteoles broadly ovate, 0.5 mm, borne immediately below flower, very rapidly caducous. Sepals 4–5.5(–6) mm, usually but not always reflexed, papillate or bearing small white scales; petals white, 7–9.5 × 2.8–4.6(–5) mm, elliptical to obovate, symmetrical or slightly asymmetrical, mostly concave in fruit; corona 1–1.4 mm; stamens 10; filaments 1.4–5 mm, sometimes irregularly fused above corona; anthers 1–1.4 mm; staminodes linear, 3–3.5 mm; style 2.4–4 mm; style branches two, 1.6–2 mm; ovary stellate, occasionally glabrous basally. Fruit subglobose, laterally compressed, 4–5 mm diam., densely stellate; seeds 2 per fruit, dark brown, broadly elliptical with 1 flattened side, 2.2–2.3 mm, irregularly shaped with few prominent ridges, surface finely striated.

Distribution, habitat, and phenology. *Dombeya danguyi* occurs in the region of Ambovombe in southwestern Madagascar on sand. Flowering collections are known from April and June and fruits from August.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya danguyi* is noted as Endangered or EN B1ab(iii)+2ab(iii). The three known collections are all from a small and unprotected area, if not from the same population; considerable habitat degradation has occurred since these collections were made.

Vernacular name. Vala (*Service Forestier 15661*).

Discussion. *Dombeya danguyi* is probably closely related to the *D. subviscosa* complex and bears a strong resemblance to *D. subviscosa* subsp. *sakarahae*; it can be distinguished from that taxon by its slightly larger flowers, with only 10 stamens and bracteole scars immediately beneath the flower rather than well below it. The buds of *D. danguyi* have an unusual elongated ellipsoid or nearly cylindrical shape, with an abruptly narrowed apex, whereas those of the *D. subviscosa* complex, like those of most species of *Dombeya* sect. *Decastemon*, are broadly ellipsoid to broadly obovoid. Another southern species with sometimes narrowly lanceolate and somewhat oblique leaves, *D. selinala*, is distinguished by stellate indument on several parts, shorter petioles, bracteole scars well beneath the flower with the pedicel sometimes thickened above, and somewhat smaller flowers with a prominent elongated corona and 15 stamens.

The flower of *Dombeya danguyi* is said to have an odor of hawthorn (*Decary 2632*).

Additional specimens examined. MADAGASCAR. **Toliara:** Ampasimpolaka, E of Ambovombe, *Decary 9049* (MO, P [2]); Sampana, Ambovombe, *Service Forestier 15661* (P [2]).

22. Dombeya digyna Hochr., Candollea 3: 33–34. 1926. TYPE: Madagascar. Mahajanga: bois, bassin du Mahajamba (Boëny), Sep. 1906 (fl.), *H. Perrier de la Bâthie 5536* (lectotype, designated by Arènes [1958: 370], P!; isolectotypes, G not seen, G image!, K not seen, K image!).

Tree to 15 m or shrub with brownish rough bark; twigs grayish to dark brown, the youngest stellate;

stipules caducous, subulate with a broad base, 2–3.6 mm, glabrate to sparsely scurfy-stellate; stipule scars on young twigs narrow, relatively long and dark. Leaves lanceolate to ovate or narrowly lanceolate, (4–)5–9.2 × (1.3–)1.8–3.4(–4) cm; petiole (2–)5–11 mm, stellate; base rounded to oblique; apex acuminate or rarely acute; margins serrulate to crenulate, with brownish glands usually located at apices of teeth; abaxial surface sparsely stellate at least along main veins, adaxial surface sparsely stellate to glabrate usually with tiny flat papillae; basal veins 5 (very rarely 3), the outer pair weak; secondary veins above base 5 to 7 per side, visible on adaxial surface, very prominent on adaxial surface; domatia usually inconspicuous but present on most large leaves in one or more pairs of secondary vein axils and often at base, those at base usually simple small hollows in vein axils, those borne in secondary vein axils also small but frequently covered, rarely domatia absent but unusually deep hollows present in vein axils. Inflorescences 2- to 4(to 8)-flowered, the larger usually an umbelliform cyme with divided peduncle, sometimes numerous and forming relatively large clusters; peduncle 2–7 mm, stellate; pedicels 5–12 mm, stellate; bracteoles caducous, occasionally persisting to anthesis, broadly oblong-elliptical to ovate or orbicular, 1.2–1.7 mm, stellate, borne immediately to slightly beneath flower. Sepals 3.2–5 mm, usually reflexed in full flower, stellate to sparsely stellate; petals 7.5–9 × 4.2–6(–6.5) mm, obovate, slightly asymmetrical to nearly symmetrical, becoming somewhat concave; corona 1–1.5 mm; stamens 15; filaments 2–3.5 mm, generally not fused above corona; anthers 0.9–1.2 mm; staminodes narrowly spatulate, 2.5–3.5 mm; style 3–4.5 mm, sparsely stellate or glabrous; style branches 2(3), 1–1.6 mm; ovary stellate. Developing fruit subglobose, possibly losing much of its indument during maturation, to 5 mm diam.

Distribution, habitat, and phenology. *Dombeya digyna* is native to dry forests on sandy soil in northwestern Madagascar; the only reported altitude is 1100–1200 m, but most localities were probably at lower altitudes. Flowering collections are known from September, February, and April and a fruiting collection from May.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya digyna* is noted as Endangered or EN B2ab(iii). Only four locations are known, none in protected areas; continued habitat degradation has been occurring in these areas, and the most recent collection is almost 40 years old.

Vernacular name. Mabolotsaka (*Service Forestier 16370*; Sakalava dialect).

Discussion. *Dombeya digyna* is distinguished from *D. tulearensis* by its somewhat longer, reliably lanceolate and acuminate leaves (whereas the so-called acuminate leaves of *D. tulearensis* have much shorter apices) and stellate ovary; the corolla is on average slightly larger, and the filaments seem to be usually free above the corona. *Dombeya digyna* also resembles *D. subviscosa* subsp. *subviscosa*, from which it may be distinguished by its more consistently and strongly stellate indument on most parts, most importantly on the sepals; additionally, *D. subviscosa* subsp. *subviscosa* usually has crenate to crenulate (though variable) leaf margins, more flowers per inflorescence, longer pedicels, and slightly smaller flowers. The limited number of collections have a broad and perhaps suspicious geographic range (that farthest to the northeast, *Gentry 11758*, was a 15 m tree, whereas that farthest to the southwest, *Service Forestier 16370*, which has very narrow leaves with prominent domatia, was a 3 m shrub). However, the existing specimens all certainly form a natural group within which it is not possible to formally recognize geographic variation, given the limited available material.

As for several other taxa (see discussion under *Dombeya aquifoliopsis*), *D. digyna* was lectotypified by Arènes (1958), who chose the P duplicate of *Perrier de la Bâthie 5536* as the type. Hochreutiner (1926) cited only the G duplicate of *Perrier de la Bâthie 5536* (no other herbarium was mentioned, and the detailed label data quoted are those of the G duplicate) and the P duplicate of *Perrier de la Bâthie 594*. Article 9.12 of the ICN (McNeill et al., 2012) implies that the cited syntype should have been chosen as lectotype in preference to an isosyntype but does not explicitly make this obligatory.

Dombeya digyna is said to have semi-soft wood used for fencing and bark with a little fiber (*Service Forestier 16370*).

Additional specimens examined. MADAGASCAR. **Mahajanga:** rd. from Antsohihy to Bealanana, 17–19 km E of Antsahabe, *Gentry 11758* (MO, P); Firingalava, *Perrier de la Bâthie 594* (P [7]); Ampandra, canton Maintirano, *Service Forestier 16370* (P [3]).

23. Dombeya micrantha Appleq., sp. nov. TYPE: Madagascar. Toamasina: Menaloha, 1952–1955 (fl.), *J. Déquaire 27753* (holotype, P!). Figure 4.

Diagnosis. Distinguished from *Dombeya subviscosa* Hochr. complex by domatia in axils of lateral veins, midrib sometimes appearing slightly sympodially branched; small-

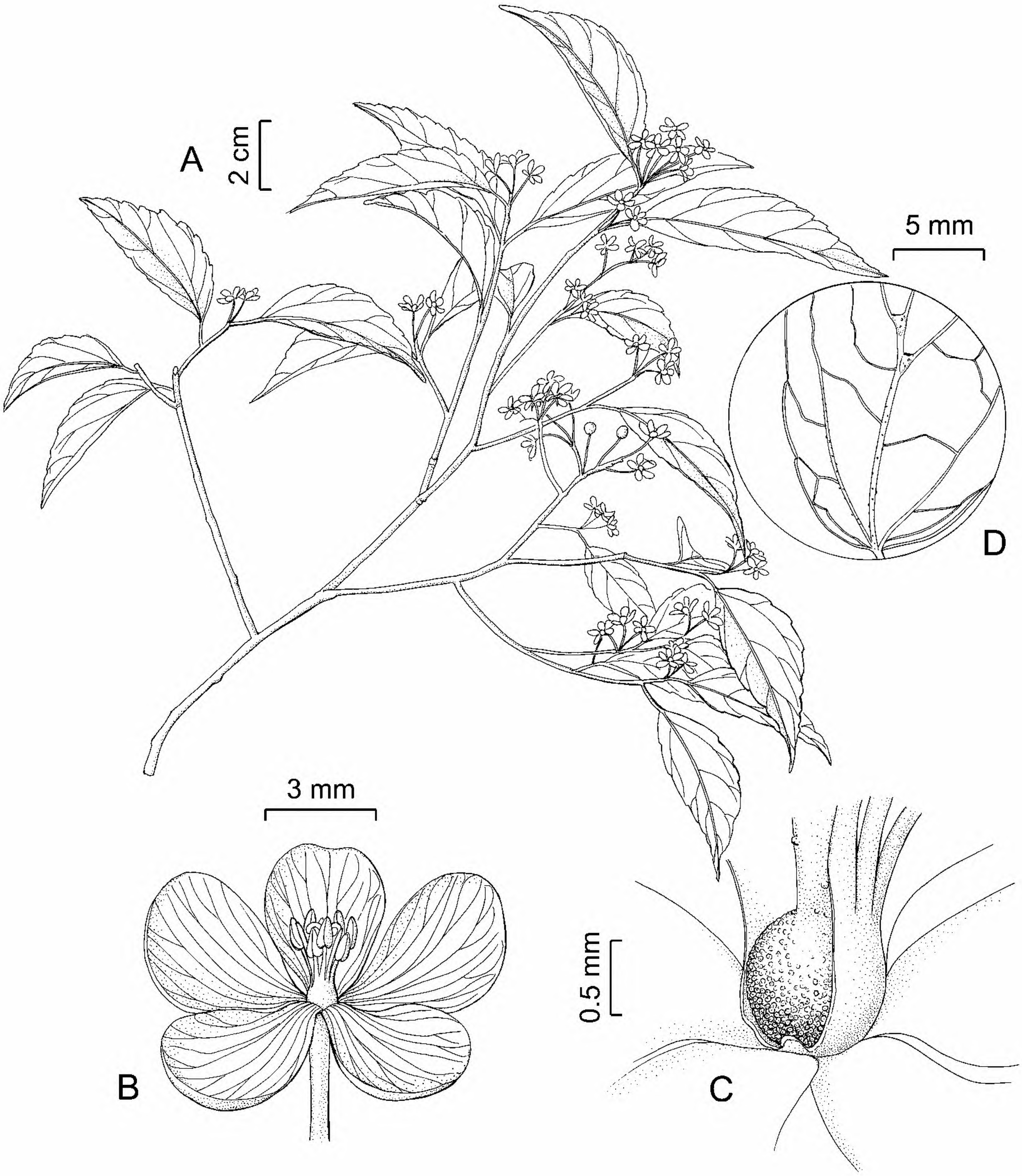


Figure 4. *Dombeya micrantha* Appleq. —A. Habit. —B. Flower. —C. Gynoecium. —D. Abaxial leaf surface. A–D from *Déquaire 27753* (P).

er flowers, with petals < 5 mm; ovary papillate, possibly becoming glabrate or glabrous after anthesis.

Tree to 10 m with grayish bark; twigs dark brown, the youngest sparsely papillate to glabrate; stipules caducous, not seen; stipule scars on young twigs narrow, inconspicuous. Leaves lanceolate, 5–7 × 1.4–2.4 cm; petiole 6–11 mm, papillate; base rounded to short-attenuate; apex acuminate, often somewhat asymmetrical; margins serrate to serrulate or crenate-serrate, with glands usually in or near tooth apices; both surfaces sparsely papillate with papillae tiny, flat, often reddish; basal veins 5(to 7), the outer weak, the inner often joining midrib well above base and running parallel to midrib rather than fusing with it; secondary veins above the base, 3 or 4 per side, slightly prominent and relatively conspicuous on both surfaces; domatia present, usually swollen and conspicuous, absent at base but present

in axils of secondary veins, the midrib sometimes having a slightly zigzag appearance and possibly sympodially branched, and also often in axils of first large tertiary veins branching from the basal veins. Inflorescences 2- to 5-flowered, sometimes borne 2 per node; peduncle 0.6–2 mm, sparsely papillate with rare single fimbriate scales; pedicels 6.5–11 mm, sparsely papillate especially above bracteole scars; bracteoles caducous, not seen, borne below midpoint of pedicel. Sepals 2.1–2.7 mm, reflexed, papillate; petals white, (3.2–)3.8–4.4 × (2–)2.4–2.8 mm, obovate, usually strongly convex at anthesis, nearly symmetrical; corona 0.6–1 mm, sometimes narrowed above ovary and slightly reflexed; stamens 10; filaments 0.5–1.6 mm, partly fused above corona; anthers yellow, 0.6–0.8 mm; staminodes linear, 1.3–2 mm; style 1.5–1.8 mm, glabrous; style branches 2, ca. 1 mm; ovary densely papillate, with indument possibly lost rapidly at least apically after flowering. Fruit not seen.

Distribution and habitat. *Dombeya micrantha* is from humid forest in the vicinity of Menaloha in eastern Madagascar.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya micrantha* is noted as Critically Endangered or CR B1ab(iii)-2ab(iii). The type locality is near Lac Alaotra and Ambatondrazaka; the region is relatively accessible and has been the source of numerous botanical collections. The fact that this species has not been recollected in over 50 years, therefore, indicates that it is quite rare.

Discussion. The affinities of *Dombeya micrantha* are uncertain. The new species is distinguished by the domatia located in axils of secondary veins and the sometimes slightly zigzag appearance of the midrib, very small flowers with petals under 5 mm, and a papillate ovary (a character not totally unknown in related species, but less common than stellate pubescence). Its strongly convex petals demonstrate that it belongs within *Dombeya* ser. *Selinala*, but it is ecologically distinctive within that series, being the only species from eastern humid forest, while all other species are native to dry seasonal western or southern forests and bush or the extreme north. It is, therefore, not plausible to hypothesize that the type is a hybrid involving another species of *Dombeya* ser. *Selinala*.

24. Dombeya parvipetala Arènes, Candollea 16: 407. 1958. TYPE: Madagascar. Toliara: Ambovombe, 3 Feb. 1931 (fl.), *R. Decary 8478* (holotype, P!; isotype, PRE not seen, PRE image!).

Shrub to 7 m or small tree; twigs pale gray, the youngest bearing small yellowish papillae; stipule scars on young twigs small, narrow to narrowly crescent-shaped, not prominent or sometimes slightly raised by outgrowth of bark proximally. Leaves narrowly lanceolate, 4.8–11 × 0.9–2.7(–3.3) cm; petiole 7–15 mm, minutely papillate; stipules caducous, narrowly lanceolate, 1.7–2.5 mm, sparsely papillate; base rounded; apex acuminate with a rounded tip; margins shallowly wavy (especially when young) or with few crenate-serrate, rounded teeth in basal part, occasionally developed into small lobes, glands often prominent toward base, absent or inconspicuous apically, located in shallow marginal concavities or in tooth or lobe apices; both surfaces sparsely flat-papillate, especially the abaxial; basal veins 5(to 7), the outer weak; main secondary veins above base 2 to 4 per side with numerous slightly smaller veins interspersed, mainly reticulodromous toward apex, visible on adaxial surface; domatia absent. Inflorescences many-flowered or less often few-flowered cymes, ± dichotomously or seldom trichotomously branched with (2)3 or 4 orders of branching, the ultimate branching sometimes umbellate with up to 7 flowers, sometimes most flowers deciduous; peduncle 0.9–3.2 cm, sparsely papillate; pedicels 3.5–9 mm, sparsely papillate; bracteoles rapidly caducous, elliptical or irregularly shaped, 0.4–0.7 mm, with sometimes papillate margins, the bracteole scars at flowering at about midpoint of pedicel or lower. Sepals (2–)2.5–3.4 mm, not reflexed, sparsely flat-papillate mostly on the lower portion, bearing large conspicuous glandular patches; petals white, 3–4.3 × 1.9–2.5 mm, obovate, slightly asymmetrical to nearly symmetrical; corona (0.5–)0.9–1.5 mm; stamens 10; filaments 0.4–1.8 mm; anthers 0.7–1.1 mm; staminodes narrowly spatulate to ligulate, 1.7–2.3 mm; style 1.7–3 mm, glabrous or with few stellate trichomes at base; style branches 2 or 3(4), 0.5–1 mm; ovary stellate with small flattish white trichomes. Fruit ellipsoid, shallowly ribbed, with a persistent style base, 3.2–4 mm high at maturity, finely white-stellate; seeds 1 per fruit, dark to reddish brown, irregularly ellipsoid, somewhat 3-sided or 4-lobed, 2.4–2.5 mm.

Distribution, habitat, and phenology. *Dombeya parvipetala* is native to southwestern and extreme southern Madagascar on sand. It flowers in January through March and fruits in February and March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya parvipetala* is noted as Endangered or EN B2ab(iii). No more than five clearly separate populations have been collected; the habitat has been subject to severe degradation, and the most recent collection (*Croat 31525*) dates to 1975.

Vernacular name. Vala (*Decary s.n.*; *Service Forestier 4535*, *14316*).

Discussion. *Dombeya parvipetala* is distinguished from most species of *Dombeya* sect. *Decastemon* by its small but consistently cymose inflorescences; it was placed by Arènes (1958) within *Dombeya* sect. *Xeropetalum*. Although no molecular data to show its affinities are available, by overall morphology this species seems to be better placed within *Dombeya* sect. *Decastemon*. Features otherwise not found within *Dombeya* sect. *Xeropetalum* include the narrowly lanceolate, acuminate leaves, solely papillate indument on all vegetative parts, nearly symmetrical petals, and staminodes that, though longer than the filaments, are shorter than the fertile stamens. Other notable features that would be very unusual in *Dombeya* sect. *Xeropetalum* include prominent leaf marginal glands and bracteole scars very low on the pedicel, as well as the relatively symmetrical inflorescence branching noted earlier.

Dombeya parvipetala is placed within *Dombeya* ser. *Selinala* because its petals are nearly symmetrical and convex, although they are unusually broad and thin textured and usually rolled or crumpled so that the tendency toward convexity is hard to see in exsiccatae. This placement is supported by other features, such as the narrowly lanceolate leaves and the unusually large and conspicuous glandular patches on the sepals, a character that is otherwise seen, in this section, only in three species of *Dombeya* ser. *Selinala* (*D. ambalabeensis*, *D. anakaensis*, and *D. sakamaliensis*). Young material of *D. parvipetala* is described as resinous (*Service Forestier 22533*).

Additional specimens examined. MADAGASCAR. **Toliara:** 1–30 km S of Beloha along road to Lavanono, *Croat 31525* (MO, P); Beloha, *Decary s.n.* (P), *Decary s.n.* (P); Ambovombe, *Decary 3505* (P), *3513* (P), *8498* (P); Jafaro–Antanimora, *Service Forestier 4535* (P [2]); Ampira–Ambovombe, *Service Forestier 14316* (MO, P [3]); forest of Analamatahitse (Analamatahotra) between Bekily and the Beraketa–Antanimora rte., *Service Forestier 22533* (MO [2], P [3]); banks of the Sakatomily E of Tsihombe, *Service Forestier 22541* (P).

25. Dombeya sakamaliensis Arènes, Candollea 16: 369. 1958. TYPE: Madagascar. Toliara: vallée de la Sakamalio, affluent de la Manambolo (bassin du Mandrare), pentes rocailleuses (gneiss), bush xérophile, 500–800 m, Dec. 1933 (fl.), *H. Humbert 13318* (holotype, P!).

Small tree; twigs dark brown, the youngest sparsely stellate; stipules caducous, lanceolate, 3 mm, sparsely stellate; stipule scars on young twigs narrow and inconspicuous. Leaves lanceolate to narrowly ovate, 6.3–9 × 2.7–3.8 cm; petiole 6–10 mm, densely stellate in young leaves, becoming sparsely stellate; base ± rounded, tending toward rounded-truncate or very slightly cordate; apex acuminate, often curving, the immediate tip rounded, or rarely acute; margins irregularly crenate-serrate, with inconspicuous glands usually in tooth apices; both surfaces sparsely stellate and bearing tiny flat papillae; basal veins 5 to 7, all but the inner pair weak; main secondary veins above base 5 to 7(to 10) per side, visible but not conspicuous on adaxial surface; domatia absent. Inflorescences 9- or 10-flowered; peduncles 3–7 mm, stellate, paired in leaf axils or divided at base, further branching in an umbelliform fashion at the apex so that a small section of peduncle may support the base of each individual pedicel; pedicels 15–19 mm, glabrate with few stellate trichomes often near base; bracteoles rapidly caducous, roughly oblong, sometimes thickened, 0.8–1 mm, stellate, at maturity bracteole scars somewhat below flower and separated from one another on pedicel. Sepals 4–5.5 mm, reflexed, papillate, with large glandular patches; petals white, 7.5–8.4 × 3.3–4 mm, obovate, strongly reflexed in flower, slightly asymmetrical, somewhat concave; corona 2.5–3.7 mm; stamens 15; filaments 0.4–1.8 mm; anthers 1–1.5 mm; staminodes linear, 2.5–3.4 mm; style 5.2–5.5(–6) mm; style branches 2, ca. 1.5 mm; ovary stellate.

Distribution, habitat, and phenology. *Dombeya sakamaliensis* has been collected in dry brush on gneiss near the Sakamalio River in southeastern Madagascar, at a reported altitude of 500–800 m; it flowers in December.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya sakamaliensis* is noted as Data Deficient or DD. Although it is known only from the type collection, botanical specimens from the area of the Mandrare River basin are quite scarce, except for Humbert's collections. Habitat quality and population status are therefore unknown.

Discussion. *Dombeya sakamaliensis* bears a strong resemblance to *D. ambalabeensis*. It is distinguished by its unusual inflorescences with

multibranched peduncles, strongly reflexed corollas, elongated pedicel above the bracteoles, and slightly larger flowers; the leaf shape and stellate ovary would also be unusual for *D. ambalabeensis*. The sepals are reflexed abruptly, rather than in a curve; since the only known specimen is at anthesis, it is unknown whether the sepals are caducous as in *D. ambalabeensis* and *D. anakaensis*. Since only one specimen exists, the possibility should be considered that it is a hybrid involving *D. ambalabeensis*; however, a second parent native to southern Madagascar that would explain the observed suite of morphological characters has not been identified.

26. Dombeya selinala Arènes, Candollea 16: 371–372. 1958. TYPE: Madagascar. Toliara: vallée moyenne du Mandrare près d'Anadabolava, forêt sèche, 200–250 m, Dec. 1933 (fl.), *H. Humbert 12512* (holotype, P!; isotypes, K not seen, K image!, MO [3]!, P!).

Dombeya cloiselii Arènes, Candollea 16: 374. 1958, syn. nov. TYPE: Madagascar. Anosy [Toliara]: Fort Dauphin, s.d., (fl.), *J. Cloisel 49* (holotype, P!).

Dombeya valafotsy Arènes, Candollea 16: 388. 1958, syn. nov. TYPE: Madagascar. Toliara: RN XI [Andohahela], distr. Fort Dauphin, forêt sèche, 7 Feb. 1951 (fl.), *Reserves Naturelles 2758* (holotype, P!; isotypes, MO!, P!).

Dombeya vohitsiombeensis Arènes, Candollea 16: 373. 1958, syn. nov. TYPE: Madagascar. Toliara: massif du Vohitsiombe, prov. Fort Dauphin, 31 July 1926 (fl.), *R. Decary 4660* (holotype, P!; isotypes, MO!, P!).

Shrub to 4 m or tree to 8 m; twigs dark brown, the youngest stellate with small white trichomes; stipules caducous, lanceolate, 1.4–2.4 mm, stellate; stipule scars on young twigs narrow, small, usually relatively inconspicuous. Leaves lanceolate to narrowly lanceolate or rarely narrowly ovate, (2.7–)4–8.1 × (0.9–)1.2–2.1(–3.2) cm; petiole 1.8–7 mm, stellate; base rounded, sometimes slightly oblique, rarely barely cordate; apex acuminate to acute; margins irregularly crenulate-serrulate to serrulate with brownish glands usually located at apices of teeth; both surfaces sparsely stellate to glabrate or occasionally papillate with small flat papillae; basal veins 5, the outer weak; secondary veins above base (4)5 to 7 per side, usually inconspicuous but visible on adaxial surface; domatia absent. Inflorescences 1- to 6(to 8)-flowered, sometimes an umbelliform cyme with divided peduncle, often numerous and forming relatively large clusters; peduncle 1.5–7 mm, stellate or rarely glabrous; pedicels (8–)12–20(–22) mm, glabrate with very few stellate trichomes basally or glabrous or occasionally papillate; bracteoles borne well below flower with pedicel sometimes thickened above bracteole scars, very rapidly caducous, oblong or ovate, 0.5–1 mm, stellate. Sepals (2.5–)3–4 mm, reflexed or not in flower, always reflexed in fruit, papillate to glabrous; petals white, (4.5–)5–6.3 × 2–3.3(–3.8) mm, elliptical, symmetrical, often strongly concave in fruit; corona (1.4–)2–2.6 mm, often erect and prominent in flower; stamens 15; filaments 0.5–1.5 mm, sometimes irregularly fused above corona; anthers yellow, 0.8–1.1 mm; staminodes narrowly spatulate, 1.8–2.4(–3) mm; style (3–)4–5.5 mm; style branches two, 0.7–1.1 mm; ovary stellate apically or glabrous. Fruit subglobose with a narrowed apex, slightly laterally compressed, 2.3–3.5 mm diam., dark brown with sparse stellate indument persisting when present on ovary; seeds 1 or 2 per fruit, dark brown, broadly oblong-elliptical to oblong-ovate, ± laterally compressed, irregularly shaped or with one side concave, 2–2.4 mm, mature seeds possibly not seen.

Distribution, habitat, and phenology. *Dombeya selinala* is native to dry forest, bush, and transitional forests in southeastern Madagascar; it has been reported to occur on gneiss, granite, laterite, and alluvial substrates at altitudes from 200 to over 500 m. Label data for the collection *Leandri 4430* give an altitude range of 400–1900 m, but no other specimen lists a maximum altitude over 800 m, so this collection is presumed to have been made in the lower part of that range. The species flowers from September through February (once in July); fruits, usually immature, are collected from December through May.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya selinala* is noted as Least Concern or LC.

Vernacular names. Androfiary (*Reserves Naturelles 6202*), lipaty (*Reserves Naturelles 8355*), seliala (*Humbert 13813* [dialect Antanosy]), selinala (*Humbert 12512*), vala (*Reserves Naturelles 2123*, *2674*, *6753*), valafotsy (*Reserves Naturelles 2758*), valomainty (*Reserves Naturelles 6209*).

Discussion. *Dombeya selinala* and *D. valafotsy* were placed in different series in Arènes' (1958) classification. The two species were distinguished largely on the observation that the former has partly stellate ovaries, while the latter has glabrous ovaries. The two are otherwise indistinguishable. The six glabrous-ovaried collections known for *D. valafotsy* represent most, but not all, of the material collected from the Andohahela area. These two names must be synonymized, and *D. selinala* is preferred because the stellate-ovaried type better reflects the common state of that character over the species' entire range. *Dombeya cloiselii* and *D. vohitsiombeensis* are each

known only from the type. Both represent poorly developed individuals of *D. selinala*; the type of *D. vohitsiombeensis* has tiny leaves, apparently due to immaturity of the specimen. Flowers of *D. selinala* are described as having a "fine" odor (*Humbert 12512*).

Additional specimens examined. MADAGASCAR. **Toliara:** Mandrare, Beza Esiva, *Descoings 2742* (MO); Andohahela RNI, Ranopiso, Mahamavo, *Eboroke 797* (MO, P); "vallée de la Sakamalio, affluent de la Manambolo," *Humbert 13331* (MO, P [2]); mont Apiky, *Humbert 13813* (MO, P [2]); Mont Vohitrandriana S of Ranopiso, *Humbert 29138* (MO, P); middle Mandrare, Anadabolava, *Keraudren 1539* (P); "haut bassin de la Mananara et abords" (SE), N d'Imonty, *Leandri 4430* (P); Anosy, Fort-Dauphin, Ankoba, *Randrianaivo et al. 1718* (MO); Anosy, Fort-Dauphin, 2.5 km E Dimonty, *Ratovoson 1544* (MO); Imonty, Behara, Androy, *Reserves Naturelles 2123* (MO [2], P [3]); Imonty, Behara, *Reserves Naturelles 2674* (P [3]); Behara, Androy, Andohahela, *Reserves Naturelles 6202* (MO, P), *6209* (MO, P [2]); Behara, Androy, *Reserves Naturelles 6753* (MO, P); Behara, Amboasary, *Reserves Naturelles 8355* (MO, P); Imonty, near Andohahela, *Service Forestier 8531* (MO, P); massif of Vohitsiandriana, N of Cap Andrahomana, *Service Forestier 11834* (MO, P [2]).

27. Dombeya sely Arènes, Candollea 16: 379–380. 1958. TYPE: Madagascar. Mahajanga: Antsingy [Bemaraha RNI], Maintirano, 24 Apr. 1952 (fl.), *Service Forestier 5276* (holotype, P!; isotypes, P [2]!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Woody plant; twigs grayish, the youngest stellate with very small scurfy trichomes; stipules lanceolate, 1.5 mm, stellate; stipule scars on young twigs narrow, inconspicuous. Leaves narrowly lanceolate to lanceolate, 3.5–5.5 × 1–1.5 cm; petiole 4–8 mm, stellate; base oblique to rounded; apex acuminate or narrowly acute; margins very shallowly serrulate to crenulate or subentire, with brownish glands located at apices of teeth; both surfaces sparsely stellate especially along main veins; basal veins 5, the outer pair weak; secondary veins above base (4)5 to 7 per side, visible on adaxial surface; domatia present on most large leaves in 2 or 3 pairs of secondary vein axils and at base. Inflorescences (1)2- or 3-flowered, often grouped in small clusters; peduncle 1–3.5 mm, stellate; pedicels 5.5–9 mm, stellate or sparsely stellate and bearing small reddish glandular papillae; bracteoles caducous, not seen, borne immediately beneath flower. Sepals 4–5 mm, reflexed, bearing small reddish glandular papillae; petals 7–8 × 3–4 mm, obovate, nearly symmetrical, concave; corona 1.5 mm, narrowed above ovary; stamens 15; filaments 2–3.5 mm, generally not fused above corona; anthers 1–1.2 mm; staminodes linear, 3–4 mm; style 4 mm, glabrous; style branches two, 1 mm; ovary densely papillate with papillae probably being lost after anthesis.

Distribution, habitat, and phenology. *Dombeya sely* is native to the vicinity of Maintirano in northwestern Madagascar; it flowers in April.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya sely* is noted as Vulnerable or VU, D. The only known locality is protected; no collections other than the type have been made, indicating that it is likely to be rare.

Vernacular name. Sely (*Service Forestier 5276*).

Discussion. *Dombeya sely* shares many characters in common with *D. digyna*, with which it co-occurs in the Maintirano region. It is distinguished by its smaller and proportionately narrower leaves (though it is possible that none of the leaves on the type collection are of mature size), somewhat smaller inflorescences with shorter peduncles, narrower petals, staminodes longer than the filaments, and a densely papillate rather than stellate ovary. *Dombeya sely* is distinguished from *D. subviscosa* subsp. *subviscosa*, the most common northwestern taxon in this section, by its small narrow leaves, staminodes exceeding the filaments, longer corona that is narrowed above the ovary, longer style, and stellate indument (which is rare in *D. subviscosa*) on most parts; both species usually have papillae on the sepals, but those of *D. sely* are reddish. The ovary of *D. subviscosa* is rarely papillate at anthesis, then apparently becoming stellate as the flower matures. Since only one collection of *D. sely* exists, the possibility that it is a hybrid involving *D. digyna* or *D. subviscosa* should be considered.

28. Dombeya subviscosa Hochr., Candollea 3: 36–37. 1926. TYPE: Madagascar. Mahajanga: moyen [haut] bassin de Bemarivo (Boïna), Feb. 1907 (fl.), *H. Perrier de la Bâthie 5511* (lectotype, designated by Arènes [1958: 370], P!; isolectotypes, G not seen, G image!, K [4] not seen, K [4] images!, TAN not seen, TAN image!).

Tree to 25 m, with DBH to 20–30(–51) cm, or large shrub; bark gray or sometimes brown; twigs grayish to brown or dark brown, the youngest papillate, small-stellate or scaly, or rarely glabrate; stipules caducous, almost never present, deltoid to lanceolate, 1–3 mm, papillate; stipule scars on young twigs narrow, often slightly prominent but small and not conspicuous. Leaves lanceolate to ovate, elliptical, narrowly

lanceolate, oblong, or oblong-oblanceolate, aberrantly obovate, (3.3–)5–11.5(–13) × 1.3–4.5(–5) cm; petiole 4–13(–16) mm, papillate, stellate, or rarely glabrate; base rounded to somewhat oblique, shallowly cordate, or rounded-truncate, sometimes attenuate at extreme base; apex acuminate to cuspidate with an often rounded tip, rarely acute or rounded; margins irregularly crenate to crenulate, occasionally tending to dentate, serrate, or sinuate-crenulate, or subentire in smaller leaves, with glands variably located, sometimes protruding; both surfaces papillate with tiny flat papillae, sometimes sparsely stellate and occasionally also bearing long unbranched trichomes mostly around midrib beneath, or rarely glabrous; basal veins 5(to 7), the outer weak; main secondary veins above base (3)4 to 6(to 8) per side, visible on adaxial surface, sometimes prominent on adaxial surface; domatia present or absent, located at base of larger leaves or rarely in axils of lower secondary veins. Inflorescences often 2(3) per node, (1)2- to 15(to 22)-flowered, the largest within each subspecies umbelliform cymes with branched peduncles; peduncle 1–13(–22) mm, the longest in cymose inflorescences; pedicels (7.5–)11–24(–28) mm; peduncle and pedicels papillate or rarely stellate with small trichomes or glabrate; bracteoles rapidly caducous, rarely present; position of bracteole scars at anthesis ranges from immediately below flower to moderately lowered (or nearly to midpoint of pedicel). Sepals (2.5–)3–5 mm, mostly to entirely reflexed by late in flower, papillate (glabrous, glaucous); petals white to cream, (4.3–)5.5–9.4 × (2–)2.4–4.3(–5) mm, obovate to elliptical, mostly concave, symmetrical or nearly so; corona 0.5–1.1(–1.8) mm; stamens 15; filaments (1.5–)2–4.5(–6) mm; anthers 0.7–1.3(–1.7) mm; staminodes linear to narrowly spatulate, 1.4–3(–3.5) mm, shorter than longest fertile filaments; style 1.5–2.5(–3.6) mm, glabrous or short-pubescent over lower portion or most of length, sometimes with stellate trichomes only at base; style branches 2(rarely 3), 0.8–2(–2.4) mm; ovary stellate at least post-anthesis, in one subspecies often partly stellate to glabrate at anthesis, very rarely papillate with few apical trichomes. Fruit subglobose, 3.3–4.5 mm diam., stellate; seeds (1)2 per fruit, dark brown, with at least 1 flattened somewhat concave side, 2–2.5 mm, surface ridged and pebbled or striated.

Discussion. As herein defined, *Dombeya subviscosa* is a highly variable species complex that encompasses five species as circumscribed by Arènes (1958, 1959). The vast majority of the morphological variation is placed within one subspecies, *D. subviscosa* subsp. *subviscosa*, which is a common and widespread taxon native to northwestern Madagascar. Synonymized species names include *D. ambongensis* Arènes, within which Arènes (1958, 1959) recognized *D. ambongensis* subsp. *sakarahae* Arènes and *D. ambongensis* var. *ihosyensis* Arènes, from southwestern and central southern Madagascar, respectively. Those two taxa are currently recognized at the subspecies level within *D. subviscosa*. Though distinctive in vegetative morphology, their floral morphology is for the most part consistent with that of *D. subviscosa* subsp. *subviscosa*.

As for some other species described by Hochreutiner (cf. *Dombeya aquifoliopsis* and *D. digyna*), the two syntypes cited in the original publication appear to have been located at G. The first of these was *Perrier de la Bâthie 5511* (for which the G duplicate is the only one seen whose label says "haut bassin du Bemarivo," as quoted by Hochreutiner [1926: 36], whereas other duplicates seen say "moyen bassin"). The second cited syntype, "Hb. Perrier, n. 31 de Jumelle," has "Boïna, Marovato, bois" given as the locality. Arènes (1958: 370) designated the P duplicate of "*Jumelle 31 (Perrier 5511)*" as the lectotype. While Perrier and Jumelle sometimes gave separate collection numbers to the same gathering while working together, in this case there is no evidence that these two collections are of a single gathering. Further, none of the known Perrier duplicates, whose images are available on JSTOR (<www.jstor.org>), are marked with a Jumelle number. Thus, Arènes not only selected an isosyntype in preference to a syntype (possibly, though not explicitly, in conflict with Art. 9.12 of the ICN [McNeill et al., 2012]) but also mistakenly conflated the two syntype collections so that it was not clear which one was meant to supply the lectotype. Since no duplicate marked *Jumelle 31* was observed during study of material at P and the locality quoted by Arènes corresponded to that from *Perrier de la Bâthie 5511* (P), the latter specimen must have been the intended lectotype and is herein treated as such.

Leaves of *Dombeya subviscosa* have been variably reported to be caducous (*Perrier de la Bâthie 5511*, *Service Forestier 19074*, *19139*, *19159*) or persistent (*Service Forestier 16938*, *19904*); field observations indicate that leaves may be deciduous but do normally persist to fruiting. The bark fiber is used to make cords (*Reserves Naturelles 1867*); the wood is used for furniture, construction, and fencing (*Service Forestier 19102*, *19139*, *19159*, *19904*) and may be considered of superior quality, as the plant has been described as "espèce de Sely mais très fort" (*Service Forestier 19102*). Flowers are reported to be eaten by the golden-crowned sifaka, *Propithecus tattersalli* (*Meyers & Boltz 126*).

Birkinshaw 1535 is likely to be a hybrid involving *Dombeya subviscosa* and resembles that species except in having densely stellate indument on all parts including the sepals, very short peduncles, and petals to 9 mm long that are nearly symmetrical but often not convex; some inflorescences are partly cymose with short branches. Among the species of *Dombeya* sect. *Decastemon*, the most plausible second parent on morphological grounds would be *D. tavia* Arènes, native to the same region, which could contribute all of the aberrant characters except inflorescence branching; however, that poorly known taxon is itself very rare and conceivably of hybrid origin. It is also possible that a species of *Dombeya* sect. *Xeropetalum* could be the second parent.

Hybrid specimen. MADAGASCAR. **Mahajanga:** Bemanevika, 6 km E Marotaolana, *Birkinshaw et al. 1535* (MO, P).

KEY TO THE SUBSPECIES OF *DOMBEYA SUBVISCOSA*

1a. Usually a tree, to 25 m; leaf marginal glands variably located, usually not at tooth apices; inflorescences (1- to)3- to 15(to 22)-flowered; bracteole scars usually not more than moderately below flower on pedicel; northwestern Madagascar ..... 28a. subsp. *subviscosa*

1b. Shrub or small tree; leaf marginal glands at tooth apices or in apical margins; inflorescences (1)2- to 5(to 10)-flowered; bracteole scars always well below flower on pedicel; southwestern to southern central Madagascar.

2a. Leaves with basal domatia usually present; blades lanceolate, occasionally to oblong, elliptical, or rarely narrowly lanceolate or ovate when young, (1.4–)2–4.5 cm broad; petals (6–)7.8–9.4 mm, probably ascending in flower..... ..... 28b. subsp. *ihosyensis* (Arènes) Appleq.

2b. Leaves with basal domatia usually absent; blades narrowly lanceolate to lanceolate or rarely ovate when young, 1.3–2.5(–3) cm broad; petals 5.5–7 mm, not conspicuously ascending ..... 28c. subsp. *sakarahae*

28a. Dombeya subviscosa Hochr. subsp. **subviscosa.**

Dombeya ambongensis Arènes [subsp. *ambongensis*] var. *ambongensis*, Candollea 16: 365–366. 1958, syn. nov. TYPE: Madagascar. Mahajanga: RN 8 [Namoroka], canton Andranomavo, distr. Soalala, terrain argileux, 30 Mar. 1953 (fl.), *Reserves Naturelles 5125* (holotype, P!; isotypes, MO!, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Dombeya ambongensis Arènes [subsp. *ambongensis* var. *ambongensis*] f. *bevazahensis* Arènes, Candollea 16: 366. 1958, syn. nov. TYPE: Madagascar. Mahajanga: Bevazaha, canton Tsaramandroso, distr. Ambato–Boeni, forêt sablonneux, 12 Feb. 1949 (fl.), *Reserves Naturelles 1867* [as "*1807*"] (holotype, P!).

Dombeya ankarafantsikae Arènes, Candollea 16: 370–371. 1958, syn. nov. TYPE: Madagascar. Mahajanga: Ankarafantsika (7e Réserve), s.d. (fr.), *Service Forestier No. 11* (holotype, P!; isotype, P!).

Dombeya boeniensis Arènes, Candollea 16: 363–364. 1958, syn. nov. TYPE: Madagascar. Mahajanga: RN 7 [Ankarafantsika], canton Tsaramandroso, distr. Ambato–Boeni, forêt sablonneux, 5 Apr. 1951 (fl.), *Reserves Naturelles 2816* (holotype, P!; isotypes, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Dombeya mafimafy Arènes, Candollea 16: 384. 1958, syn. nov. TYPE: Madagascar. Mahajanga: Andapinarosy, Befandriana–Nord, 2 Mar. 1957 (fl.), *Service Forestier 3342* (holotype, P!; isotypes, P [2]!).

Dombeya subviscosa var. *brevistaminodia* Arènes, Candollea 16: 370. 1958, syn. nov. TYPE: Madagascar. Mahajanga: RN 7 [Ankarafantsika], canton Tsaramandroso, distr. Ambato–Boeni, 5 Apr. 1951 (fr.), *Reserves Naturelles 2828* (holotype, P!; isotypes, P!, TAN [2] not seen, TAN [2] images!).

Tree to 25 m, with DBH to 20–30(–51) cm, rarely a shrub; bark mottled gray, sometimes becoming brown and strongly furrowed on all or part of trunk; twigs grayish to brown or dark brown, the youngest papillate, stellate with small, sometimes scaly trichomes, or rarely glabrate. Leaves lanceolate to ovate or elliptical, occasionally somewhat oblong, seldom to oblong-oblanceolate or aberrantly obovate, 5–10.6(–13) × 1.6–4.3(–5) cm; petiole 4–12(–16) mm, papillate or stellate; base usually rounded, occasionally oblique, shallowly cordate, or rounded-truncate, rarely attenuate at extreme base and then domatia never present; apex acuminate to cuspidate with an often rounded tip, very rarely rounded or acute; margins irregularly crenate to crenulate, subentire in smaller leaves, or rarely crenate-dentate, with glands variably located between teeth or in apical margins of teeth, seldom in tooth apices; both surfaces papillate, sometimes sparsely stellate and occasionally also bearing long unbranched trichomes mostly around midrib beneath, or glabrous; basal veins 5(to 7); main secondary veins above base (4)5 or 6(to 8) per side, in small/young leaves not prominent on abaxial surface, in larger leaves somewhat prominent; domatia often present at base of larger leaves, occasionally in axils of lower secondary veins, small but often well developed, surrounded by unbranched trichomes. Inflorescences (1- to)3- to 15(to 22)-flowered; peduncle (1.5–)4–13(–22) mm; pedicels (7.5–)11–23(–28) mm; peduncle and pedicels papillate or rarely stellate with small trichomes, sometimes papillate on otherwise stellate individuals; bracteoles 0.7–1.1 mm, broadly deltoid, papillate; position of bracteole scars at anthesis ranges from immediately below flower to moderately lowered, very rarely nearly to midpoint of pedicel. Sepals (2.5–)3–4.2(–4.6) mm, papillate or less often glabrous or glaucous; petals (4.3–)5.5–8(–8.3) × (2–)2.4–

4(–4.6) mm; filaments (1.5–)2–4.5 mm; staminodes 1.4–2.4(–3.5) mm; style glabrous or bearing short straight trichomes over lower portion or most of length, sometimes with stellate trichomes only at base; style branches 2(rarely 3), 0.8–1.5(–2.4) mm; ovary stellate post-anthesis, in early flower ranging from glabrate except for a few trichomes at base of style to stellate only apically or stellate throughout, or very rarely papillate with trichomes at apex and style base. Fruit subglobose, somewhat vertically compressed or broadest at base; seeds (1)2 per fruit, irregularly shaped, ranging from roughly ovate-elliptical to elliptical, broadly oblong or suborbicular, surface ridged and striated.

Distribution, habitat, and phenology. *Dombeya subviscosa* subsp. *subviscosa* occurs in dry forests of northwestern Madagascar at elevations from 2 to at least 293 m. Reported substrates include black, red, and yellow sand, gneiss, and less frequently limestone. It flowers from February to May and fruits from April to June (seldom in March).

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya subviscosa* subsp. *subviscosa* is noted as Least Concern or LC.

Vernacular names. Mafimafy (*Service Forestier 3342*, *5876*, *15081*, *16938* [Tsimihety dialect], *18536*, *19074* [Tsimihety dialect], *19102* [Tsimihety dialect]), mananjara (*Reserves Naturelles 5408*), seliala (*Reserves Naturelles 10305*), selibe (*Reserves Naturelles 10289*), selimalitalita (*Reserves Naturelles 1867*, *Service Forestier* [?] *No. 17*), selivato (*Applequist et al. 275*, *Service Forestier 3556*, *5357*, *19139* [Marofotsy dialect], *19159* [Marofotsy dialect]), sely (*Resereves Naturelles 10070*, *Service Forestier 10392*, *19904*), sely ara (*Service Forestier 3489*), sely malalihy (*Meyers & Boltz 126*), voambarihy (*Reserves Naturelles 5125*).

Discussion. *Dombeya subviscosa* is probably closely related to *D. ambohitrensis* and *D. vohemarensis*, both native to extreme northern Madagascar and similar enough to be confused with *D. subviscosa* subsp. *subviscosa*. *Dombeya ambohitrensis* has pedicels to 12(–16) mm, narrower petals (not exceeding 2.5 mm broad), a glabrous style, and an ovary that is papillate throughout fruit development. *Dombeya vohemarensis* is distinguished by its shrubby habit, sinuate leaf margins, very low bracteole scars, longer and usually not reflexed sepals, and staminodes about equal to the longest filaments.

The *Dombeya subviscosa* subsp. *subviscosa* complex was treated as five distinct species by Arènes (1958, 1959) and is wide ranging and extremely diverse in morphology. Variable characters include leaf shape, width of the leaf base and conformation of the apex, indument of vegetative parts, number of flowers per inflorescence, pedicel length, position of bracteole scars, and corona length. Within the presently available material, there do not seem to be identifiable suites of characters. A broad range of combinations of character states can be seen, which implies that any subgroups involved are not reproductively separated. Morphological change over the growing season may exacerbate taxonomic confusion. Young leaves are fairly consistent in appearance, being lanceolate to narrowly ovate, sometimes tending to oblong, with an acuminate apex, subentire margins, and weak venation. Mature leaves, which have much stronger venation and marginal crenation, vary from ovate and acuminate to broadly ovate or elliptical with a broad base and short-acuminate or cuspidate apex or narrower and more oblong with a very long narrow acuminate apex. On specimens representing all of these mature forms, similar-looking young leaves can be seen, and the form of mature leaves also varies within individuals as well as regions. At flowering, all leaves are often young, whereas fruiting specimens often have largely mature leaves and, therefore, may appear quite different. Another confusing factor is that while the fruit is almost always stellate, the ovary of most specimens in early flower initially bears stellate trichomes only apically, the basal portion apparently becoming stellate only after anthesis. In all other taxa of *Dombeya* sect. *Decastemon* with stellate ovaries, the indument is well developed by the time of anthesis.

Dombeya subviscosa subsp. *subviscosa* as herein circumscribed includes both *D. boeniensis* and *D. ambongensis* var. *ambongensis* as synonyms. Arènes (1958, 1959) placed the latter two in a different subseries based on the fact that the petioles were glabrous rather than being stellate when young (specimens with mature leaves are less likely to display stellate pubescence). However, this character can vary even within a single plant. *Dombeya boeniensis* and *D. ambongensis* were distinguished by differences in their leaf shape; the material now available suggests that variation in leaf shape between those two forms (which do not represent the extremes of the range) is essentially continuous. Most collections fall into this group, which would appear quite variable even if specimens with exceptionally broad leaves or basally positioned bracteoles (see below) were excluded due to variation in pubescence, number of flowers, length of pedicels, etc. *Dombeya ambongensis* f. *bevazahensis*, defined by

the supposed absence of staminodes, falls into this group; it was described from two specimens that are in rather poor condition, but at least some flowers on each do have staminodes.

Dombeya subviscosa var. *brevistaminodia* was supposedly distinguished by its unusually short staminodes, but the mounted material has only maturing fruit without intact androecia, leading to the suspicion that damaged flowers have been misinterpreted or that the fragments of a flower barely post-anthesis in the fragment packet of the type specimen may have been mixed up. However, the type is one of the few specimens with mature leaves that are broadly elliptical with cuspidate apices. Segregation of those specimens at some level may be appealing, but is so far unsupported by other characters; therefore, this variety is synonymized under the autonymic subspecies of *D. subviscosa*.

The approximate position of bracteole scars on the pedicel at and after anthesis is usually consistent among specimens included within the *Dombeya subviscosa* subsp. *subviscosa* group. However, three collections (*Service Forestier No. 142*, *10392*, and *19904*) have bracteole scars borne very low on the pedicel as is seen in *D. subviscosa* subsp. *sakarahae* or *D. subviscosa* subsp. *ihosyensis*, or perhaps the related species *D. ambohitrensis* and *D. vohemarensis*. These collections all have immature leaves and rather few and small flowers (petals not over 6.5 mm). One is from the Ankarafantsika region, where other more typical specimens have also been collected; the other two represent the only known collections from Maintirano. No other characters have yet been found to distinguish these specimens from existing material of the *subviscosa* group.

Dombeya mafimafy, described from a single specimen, was distinguished by its papillate ovary. The holotype *Service Forestier 3342*, in early flower, also frequently has a few trichomes at the juncture of ovary and style, as is seen in the young flowers of *D. subviscosa* subsp. *subviscosa* collections with late-developing indument. The ovary ranges from glabrate to scaly (with most flowers barely at anthesis), and the corona is unusually long. *Dombeya mafimafy* otherwise appears consistent with *D. subviscosa* subsp. *subviscosa* and is probably interpretable as an aberrant individual of that subspecies, or at most a local variant; the name is, therefore, synonymized.

Dombeya ankarafantsikae, also described from a single specimen (*Service Forestier No. 11*), was distinguished by its narrow petals and by stamens putatively occurring in groups of two or three, therefore, sometimes fewer than 15. The type specimen is fruiting, and material is not adequate to confirm this variation in stamen number. The specimen is much more remarkable because its sepals are mostly not reflexed, and its leaf morphology is rather unusual. However, as noted, more typical populations of *D. subviscosa* also occur in and around Ankarafantsika, and recent collections by the author in several forests in that area did not relocate any populations with comparable morphology. The best placement of *D. ankarafantsikae* lies within the synonymy of *D. subviscosa* subsp. *subviscosa*.

Additional specimens examined. MADAGASCAR. **Antsiranana:** Antsahalalina, 12 km E of Daraina, *Meyers & Boltz 126* (MO, P). **Mahajanga:** Ankarafantsika Natl. Park, *Applequist et al. 269*, *270*, *271*, *272*, *273*, *274*, *276* (G, MO, P, TAN, US); SE of Ankarafantsika Natl. Park, *Applequist et al. 275* (MO, P, TAN); Mariarano, N of Mahajanga, *Applequist et al. 277* (G, MO, P, TAN, US); Maevatanana–Berivotra, *Descoings 3482* (MO [2]); Tsaratanana RN 4 between Ampijoroa and Andranofasika, *Dorr & Koenders 3057* (MO, P); Ankarafantsika, *Gentry & Schatz 62096* (MO); H[aut] Bemarivo (Boïna), *Perrier de la Bâthie 2282* (P [2]); Marovato (Boina), *Perrier de la Bâthie 12166* (P); Ankarafantsika RN, Tsaramandroso, *Reserves Naturelles 2921* (P [2]); Namoroka RN, Andranomavo, Soalala, *Reserves Naturelles 5408* (MO, P [3]); Andranomavo, Soalala, *Reserves Naturelles 7351* (MO, P [2]); Antsalova, *Reserves Naturelles 10070* (P [3]); W of Antsalova, *Reserves Naturelles 10289* (MO, P [4]); Antsalova, *Reserves Naturelles 10305* (P [5]); Bevazaha, *Service Forestier* [?] *No. 17* (P [3]); Namoroka, *Service Forestier No. 28* (MO, P); Bevasaha, Ankarafantsika, *Service Forestier No. 142* (P); Ambaindahy, Ambolomoty, *Service Forestier 3489* (P); Ampijoroa, Ankarafantsika, *Service Forestier 3556* (P); Besalampy, *Service Forestier 5357* (MO, P); Mitsinjo, *Service Forestier 5744* (MO [2], P); Ampandrana, Port Bergé, *Service Forestier 5876* (P); Antanandava, near Maintirano, *Service Forestier 10392* (MO [4], P [3]); Analahefina, Antonibe, Analalava, *Service Forestier 15081* (MO, P [4]); Bora, Ampombilava, Antsohihy, *Service Forestier 16938* (MO, P); Androhimenabe, NE of Amparihimikimbo (E of the Baie de Narinda), *Service Forestier 18536* (MO, P [2]); Antsahamangitrika, Mahalina, Tsarahonenana, *Service Forestier 19074* (P); Tsimaimborano, Marovato, Antonibé, *Service Forestier 19102* (MO, P [2]); Ampasindava, Tsaratanana, *Service Forestier 19139* (MO, P), *19159* (P [2]); rte. Marofandroboaka–Mitsinjo, *Service Forestier 19486* (MO, P); Beabata, Ambiky, Maintirano, *Service Forestier 19904* (P).

28b. Dombeya subviscosa Hochr. subsp. **ihosyensis** (Arènes) Appleq., comb. et stat. nov. Basionym: *Dombeya ambongensis* Arènes [subsp. *ambongensis*] var. *ihosyensis* Arènes, Candollea 16: 366. 1958. TYPE: Madagascar. Fianarantsoa: vestiges de forêts tropophylles, dans la vallée de la Menarahaka, à l'E d'Ihosy, Feb. 1955 (fl.), *Service Forestier 11638* (holotype, P!; isotypes, MO [2]!, P [2]!, TEF not seen, TEF image!).

Large shrub; twigs grayish brown, the youngest minutely papillate. Leaves lanceolate, occasionally tending to oblong or elliptical, very rarely to ovate

especially in young leaves, 6–11.5 × (1.4–)2.3–4.5 cm; petiole 6–13 mm, papillate, occasionally with a few flat-stellate trichomes, or rarely stellate when young; base somewhat oblique, rarely somewhat rounded-truncate to rounded; apex acuminate or rarely acute with a rounded tip; margins irregularly crenate to crenulate or crenate-serrulate (to sinuate), with glands located in apices or apical margins of teeth; both surfaces papillate, rarely sparsely stellate especially when young; basal veins 5(6 or very rarely 7); main secondary veins above base 4 or 5(to 7) per side, prominent on abaxial surface; domatia usually present at base, well developed with a "roof" and sparse unbranched trichomes. Inflorescences 2- to 5(to 8)-flowered; peduncle 1.5–6 mm, papillate; pedicels (15–)18–24 mm, papillate with whitish or occasionally reddish papillae; bracteoles not seen, bracteole scars at anthesis well below flower on pedicel. Sepals 4.3–5 mm, papillate; petals (6–)7.8–9.4 × 3.6–4.3(–5) mm, probably ascending in flower; filaments 3.5–6 mm; staminodes 2–3 mm; style glabrous or with few small trichomes at base; style branches two, 1.5–2 mm; ovary stellate. Fruit possibly subglobose, slightly compressed, 4–5 mm; mature seeds unknown.

Distribution, habitat, and phenology. *Dombeya subviscosa* subsp. *ihosyensis* is native to dry forests in southern Madagascar; the only reported altitude is 700–800 m. Its usual substrate is sand, though the aberrant *Service Forestier 26046* (discussed below) was collected on red lateritic soil. It flowers in January and February and fruits in March; *Service Forestier 26046* flowered in early March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya subviscosa* subsp. *ihosyensis* is noted as Endangered or EN B1ab(iii)+2ab(iii). Only two localities are known; one atypical specimen is from a protected area, but the other existing collections (all made in 1955) were from a previously existing forest near Ihosy that has suffered serious degradation and is now essentially gone. No recent collections have been made.

Discussion. *Dombeya subviscosa* subsp. *ihosyensis* is distinguished from the autonymic *D. subviscosa* subsp. *subviscosa* by its more conspicuous domatia, smaller inflorescences, lowered bracteole scars, and usually larger, strongly ascending petals. Although this subspecies is very rare, morphological variation is problematically great. The only specimen not from Menarahaka, *Keraudren 462*, bears significant stellate indument on the leaves; its leaves have often symmetrical bases and few, small domatia. The specimen is only in bud, so its identity might be questionable; however, it cannot be identified as *D. subviscosa* subsp. *sakarahae* or any other species in the section. The leaves appear immature, and immature leaves may have stellate trichomes that are later lost. This specimen is only tentatively identified as *D. subviscosa* subsp. *ihosyensis*. *Service Forestier 13789* from Menarahaka, the only fruiting specimen seen, has small and narrow leaves with sometimes sinuate margins, a heavily papillate indument, and shorter petals (6 × 3.5–4 mm vs. 7.8–9.4 mm in other specimens from the area). This specimen is herein interpreted as an unusual individual, or potentially a hybrid.

Service Forestier 26046, a specimen in early anthesis with few flowers in poor condition, strongly resembles *Keraudren 462* but with a more strongly stellate indument, as well as short unbranched trichomes on the lower leaf surface and sometimes reddish papillae on most parts; it has no domatia. Though the vegetative appearance is more similar to *Dombeya subviscosa* subsp. *ihosyensis* than to any other known taxon from the region, the petals are short and broad (6.5 × 4.1 mm), the style branches and filaments are short, and the bracteoles are borne immediately below the flower. This specimen may represent a hybrid between *D. subviscosa* subsp. *ihosyensis* and another species from the region, most likely *D. ambalabeensis*.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** high valley of the Menarahaka E of Ihosy, 28 Jan. & 10 Apr. 1955, *Humbert 28596* (P); Menarahaka, Ihosy, 28 Jan. 1955, *Service Forestier 13736* (P); Menarahaka, Ihosy, 20 Mar. 1955, *Service Forestier 13789* (P). **Toliara:** Zombitsy, near Sakarafaka, Mar. 1960, *Keraudren 462* (P).

Hybrid specimen. MADAGASCAR. **Toliara:** Analamaribe, near Analamary, Ianakafy, *Service Forestier 26046* (P).

28c. Dombeya subviscosa Hochr. subsp. **sakarahae** (Arènes) Appleq., comb. nov. *Dombeya ambongensis* Arènes subsp. *sakarahae* Arènes, Candollea 16: 366. 1958. TYPE: Madagascar. Toliara: Analamary, Sakaraha, 22 Jan. 1951 (fl.), *Service Forestier 2810* (holotype, P!; isotypes, TAN not seen, TAN image!, TEF not seen, TEF image!).

Dombeya ambongensis [subsp. *sakarahae*] var. *fandrareensis* Arènes, Candollea 16: 367. 1958, syn. nov. TYPE: Madagascar. Toliara: plateau calcaire au N du Fiherenana, forêt sèche de Fandrare a 40 km NE de Tulear, vers 400 m, Mar. 1934 (fl.), *H. Humbert 14333* (holotype, P!; isotype, P!).

Small tree, or much-branched shrub to 5 m with DBH to 5 cm; bark grayish; twigs grayish brown, the

youngest minutely scaly to sparsely papillate or glabrate. Leaves narrowly lanceolate to lanceolate, very rarely to ovate especially in young leaves, 3.3–8.5 × 1.3–2.5(–3) cm; petiole 3–10(–12) mm, flat-papillate to glabrate, occasionally with a few flat-stellate trichomes; base rounded to shallowly cordate or oblique; apex acuminate or rarely acute; margins irregularly sinuate-crenulate to crenate, crenate-dentate, or serrate with usually rounded teeth, with glands located in apices or apical margins of teeth; both surfaces papillate to glabrate, sometimes with rare stellate trichomes; basal veins 5; main secondary veins above base (3)4 or 5(6)per side, not prominent on abaxial surface; domatia usually absent, rarely present at base. Inflorescences (1)2- to 4(to 10)-flowered, sometimes numerous and forming relatively large clusters; peduncle 1–6.5(–10) mm, papillate to glabrate; pedicels (12–)16–20 mm, papillate or rarely glabrate; bracteoles broadly ovate, ca. 0.5 mm, bracteole scars at anthesis well below flower on pedicel. Sepals 3.6–4.5(–5) mm, papillate; petals 5.5–7 × 2.5–3.5(–4.1) mm; filaments (2–)3–4.5 mm; anthers 1–1.3(–1.5) mm; staminodes 1.5–2.8 mm; style basally stellate or glabrous; style branches two, 1–2 mm; ovary stellate. Fruit subglobose, stellate; seeds 2 per fruit, roughly hemispherical, surface slightly pebbled and minutely ridged.

Distribution, habitat, and phenology. *Dombeya subviscosa* subsp. *sakarahae* is native to dry forests in southwestern Madagascar, on both white sand and limestone at altitudes of 35–850 m. It flowers from January to March and fruits from March to June.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya subviscosa* subsp. *sakarahae* is noted as Vulnerable or VU B1ab(iii)+2ab(iii). Fewer than 10 localities are recorded, only one in a protected area, and severe habitat degradation has occurred in its native range.

Vernacular names. Faikafotse (*Service Forestier 2810*), sarivala (*Service Forestier 11921*).

Discussion. *Dombeya subviscosa* subsp. *sakarahae* is distinguished, though not altogether reliably, from the other two subspecies by its usually narrower leaves that seldom have domatia. It is further distinguished from *D. subviscosa* subsp. *subviscosa* by its fewer-flowered inflorescences and lowered bracteole scars, and from *D. subviscosa* subsp. *ihosyensis* by its smaller flowers (petals 5.5–7 mm vs. [6–]7.8–9.4 mm), with petals not ascending. *Dombeya anakaensis* also has often narrowly lanceolate leaves and occurs in southwestern Madagascar; it lacks papillae on the inflorescences and has bracteole scars immediately below the flower, staminodes usually longer than the filaments, and a papillate ovary, as well as the distinctive calyx morphology in fruit that it shares with *D. ambalabeensis*.

Arènes (1958, 1959) recognized *Dombeya ambongensis* var. *fandrareensis* based primarily upon the presence of small caducous stellate trichomes on the leaves of the type. The name is synonymized because this and other characters are in fact variable within this taxon's relatively continuous range (e.g., one leaf on the type of *D. ambongensis* subsp. *sakarahae* bears stellate trichomes).

Service Forestier 11921, a specimen in early flower, is suggested to be a hybrid of *Dombeya subviscosa* subsp. *sakarahae* × *D. anakaensis*. The specimen resembles the former taxon except in having inflorescences with up to seven or eight flowers on thickened peduncles, bracteoles borne close to the receptacle, shorter pedicels (as little as 7.5 mm in full flower), smaller flowers (petals 4–5.5 × 1.5–2.1 mm), and shorter filaments (1–1.8 mm vs. staminodes 1.5 mm). These characters are generally consistent with *D. anakaensis* parentage.

Additional specimens examined. MADAGASCAR. **Toliara:** Zombitsy, 10.1 km NE of Sakaraha, *Barnett 509* (MO); 45–55 km E of Tulear on rd. to Andranovory, *Croat 31072* (MO, P); "S de la forêt d'Analafanja au N du Fiherenana, plateau au S de Mitsinjy," *Humbert 14316* (P [2]); Beandro, 55–60 km NE of Tulear, *Humbert 29552* (P); Zombitsy (Sakaraha), *Humbert et al. 29562* (MO, P); 55 km NE of Morondava via Rte. 8, Kirindy Forest, *Noyes et al. 1018* (P); Morondava, *Rahantamalala 188* (P); Zombitsy, *Service Forestier 18598* (P [3]).

Hybrid specimen. MADAGASCAR. **Toliara:** Zombitsy, *Service Forestier 11921* (MO, P [2]).

29. Dombeya tulearensis Arènes, Candollea 16: 380–381. 1958. TYPE: Madagascar. Toliara: RN X [Tsimanampetsotsy], distr. Tulear, 28 Feb. 1950 (fl.), *Reserves Naturelles 2509* (holotype, P!; isotypes, MO!, P!).

Dombeya meneriky Arènes, Candollea 16: 381. 1958, syn. nov. TYPE: Madagascar. Toliara: massif de Vohitsiandriana, au N du Cap Andrahomana, vers 350 m, Mar. 1955 (fl.), *Service Forestier 11836* (holotype, P!; isotype, P!).

Tree to 9 m, DBH to 20 cm, much branched, or a shrub to 5 m, with smooth gray bark; twigs grayish to dark brown, the youngest stellate with small reddish (very rarely mostly white) trichomes; stipules caducous, deltoid-acuminate to lanceolate-acuminate or ovate, 2–3 mm, stellate; stipule scars on young twigs narrow, sometimes moderately prominent, inconspic-

uous or dark. Leaves quite variable in shape, very often somewhat oblong, ranging from oblong-elliptical to narrowly ovate or lanceolate, elliptical, oblong-oblanceolate, or rarely narrowly elliptical, 3.5–7.2 × (1–)1.5–2.6(–3.2) cm; petiole (4–)6–12(–16) mm, reddish or rarely pale stellate; base oblique or rounded and sometimes tapering at the extreme base; apex acute to short-acuminate, rounded, or rarely emarginate; margins variably small-toothed or shallowly wavy, often subentire, with brownish glands usually located at apices of teeth; both surfaces sparsely reddish to pale stellate; basal veins (4)5(to 7), all but the innermost pair weak, the innermost pair often decurrent from midvein; secondary veins above base 3 to 5 per side, visible on abaxial surface, very prominent on adaxial surface; domatia usually inconspicuous but present on most large leaves in one or more pairs of secondary vein axils and often at base, those at base usually simple small hollows in vein axils, more likely to be present when leaf base is relatively symmetrical, those borne in secondary vein axils also small but frequently covered. Inflorescences 2- to 7(to 9)-flowered, sometimes an umbelliform cyme with divided peduncle or rarely a few-flowered condensed cyme, sometimes numerous and forming relatively large clusters; peduncle 1.5–7.5 mm; pedicels (5.5–)7–15 mm; peduncle and pedicels stellate, the trichomes pale red to nearly white; bracteoles caducous, rarely persisting to anthesis, ovate to broadly elliptical or deltoid, often cuspidate or short-acuminate, 1–1.6(–2.5) mm, stellate, borne immediately beneath flower. Sepals (3.7–)4.2–5.2(–7) mm, usually reflexed in flower, reflexed and then dehiscent in fruit, papillate to glabrous or rarely with some stellate trichomes; petals white to cream, (5.6–)6–8(–9) × (3–)3.5–5(–5.8) mm, elliptical to obovate, moderately asymmetrical to nearly symmetrical, mostly concave in fruit, at anthesis no more than slightly concave around apical margin; corona 1.4–2(–2.4) mm, often narrowed above ovary; stamens 15; filaments (0.7–)2–4.8 mm, sometimes irregularly fused above corona; anthers 0.9–1.3 mm; staminodes narrowly spatulate or rarely linear, 2.5–4(–5.5) mm, almost always shorter than the longest fertile stamens; style 2.8–4(–5.2) mm; style branches two, 0.8–1.5 mm; ovary dark, papillate. Fruit broadly ellipsoid to subglobose with a narrowed apex at least during development, at least sometimes globose at maturity, (4–)5–6 mm diam., blackish at maturity when dried but reportedly green when fresh, papillate; seeds 1 per fruit, dark brown, 3.5 mm, irregularly shaped, broadly ellipsoid, with 3 sides deeply sunken or possibly laterally compressed, surface minutely ridged and sometimes appearing papillate.

Distribution, habitat, and phenology. *Dombeya tulearensis* is native to dry (or seldom subhumid) forest and brush in southern Madagascar, on sand or rock, including granite, sometimes along waterways, at altitudes of 100–1000 m. It flowers from December to March (rarely to May) and fruits from February to May (rarely in January).

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya tulearensis* is noted as Least Concern or LC.

Vernacular names. Hazofotsy (*Reserves Naturelles 6207*), kambahy (*Reserves Naturelles 2505bis*), mandoavato (*Reserves Naturelles 2509*), mandohavato (*Reserves Naturelles 2760*), meneriky (*Humbert 13047*; dialect Antandroy), valafotsy (*Service Forestier 5293*).

Discussion. *Dombeya tulearensis* was distinguished from *D. meneriky* by Arènes (1958) based on variation in stipule and bracteole morphology and the occurrence of rare trichomes on the sepals of *D. tulearensis*; the two are clearly conspecific. The two epithets have equal priority; *D. tulearensis* is preferred because it may have been slightly more often used and seems more informative (Tulear being a familiar locality in Madagascar).

Flowers of *Dombeya tulearensis* are reported to be sweet-scented (*Boiteau 2533*, *Du Puy & Du Puy MB560*) and frequented by bees (*Du Puy & Du Puy MB560*). The stem may also have a distinct scent (*Randriamampionona 117*).

Service Forestier 22625, which comes from an area where typical *Dombeya tulearensis* has been collected, has very large (to 9.4 cm) ovate to lanceolate leaves, with acuminate to cuspidate apices, crenate-serrate margins with conspicuous rounded teeth, and an unusual number of basal and secondary veins. The inflorescences are up to 10-flowered, and those with the most flowers tend to be cymose, though without elongated internal branches; the flowers are slightly larger than typical of *D. tulearensis*. This specimen is suggested to be a hybrid between *D. tulearensis* and another species of *Dombeya*, possibly belonging to *Dombeya* sect. *Xeropetalum* rather than *Dombeya* sect. *Decastemon*. Putative hybrids involving *D. tulearensis* and other species of *Dombeya* sect. *Decastemon* have been otherwise noted.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** Ihosy, Bemanda, *Cours 5126* (MO, P); Ihosy, *Humbert 14453* (P); Horombe plateau, near inter-

section of routes from Ihosy to Fort Dauphin and Tuléar, *Service Forestier 22604* (P). **Toliara:** Bevilany, *Boiteau 2533* (MO, P); SE coast, *Descoings 628, 649* (MO); NE of Amboasary, N of Ankilitelo, 5 km N of RN 13, *Du Puy & Du Puy MB560* (MO, P [2]); Andohahela RNI, Ranopiso, *Eboroke 812* (MO, P); valley of the Manambolo, left bank, Isomono, monts Kotriha and Isomonobe, *Humbert 12807* (MO, P [2]); valley of the Manambolo, right bank, Isomono, *Humbert 13047* (MO, P [5]); mont Vohitrandriana S of Ranopiso, *Humbert & Capuron 29152* (MO, P); Zombitsy, *Humbert et al. 29659* (P); Andohahela, parcelle 3, *Phillipson & Milijaona 3532* (MO); "entre le rite de l'hombre et Fort Dauphin," *Rabevohitra 2231* (MO, P); Andohahela, parcelle 3, *Randriamampionona 117* (MO, P); Andohahela, parcelle 3, *Randriamampionona 288* (MO, P); Tsimelahy, near Andohahela parcelle 2, 9 km N of Karera, *Randrianaivo et al. 97* (MO, P); Anosy, Ankoba, 12 km NE of Ambatoabo, *Randrianaivo et al. 1549* (MO); Tsimanampetsotsy RN, *Reserves Naturelles 2505bis* (P [3]); Andohahela, *Reserves Naturelles 2760* (P [3]); RN XI, canton Behara, distr. Androy, *Reserves Naturelles 6207* (MO, P); Zombitsy Natl. Park, Ambakitany, N of Natl. Rte. 7, *Rogers et al. 850* (MO); Anjiozio, Vohimainty, Behara, *Service Forestier 5293* (P [2]); massif of Vohipary, NW of Andalatanosy (Antanimora), *Service Forestier 22497* (MO, P).

Hybrid specimen. MADAGASCAR. **Fianarantsoa:** basin of the Menarahaka, near intersection of routes from Ihosy to Ivohibe and Iakora, *Service Forestier 22625* (MO, P).

30. *Dombeya vohemarensis* Appleq., sp. nov. TYPE: Madagascar. Antsiranana: fivondronana Vohémar, firaisana Nosy Be, fokontany Anjiabe, forêt d'Analabe, 13°04′43″S, 049°54′04″E, 11 May 2004 (fr.), *D. Rabehevitra, R. Razakamalala & Mathieu 941* (holotype, MO!; isotypes, P!, TEF not seen). Figure 5.

Diagnosis. Differs from *Dombeya subviscosa* Hochr. subsp. *subviscosa* in having a shrubby habit, leaves with sinuate margins, bracteole scars on pedicel in fruit well below receptacle, sepals longer (5–6.5 mm) and mostly not reflexed, staminodes similar in length to filaments of fertile stamens.

Shrub to 5 m or tree to 12 m, with DBH to 10 cm; twigs grayish or dark brown, the youngest papillate with minute papillae or small flat scales; stipules caducous, lanceolate, 1–1.6 mm, papillate or scaly; stipule scars on young twigs usually small, inconspicuous, dark, but sometimes prominent with the extreme base of stipule appearing to persist (very broad pale scars at nodes are bud or peduncle scars). Leaves ovate to lanceolate or oblong-ovate, 5–8.5 × 1.8–4 cm; petiole 5–11 mm, minutely papillate; base rounded to shallowly cordate, in most large leaves shallowly cordate; apex acuminate or occasionally cuspidate with a rounded tip; margins irregularly sinuate to crenate-sinuate, with glands usually located on apical side of marginal convexities, often protruding especially near leaf apex; both surfaces papillate with tiny flat papillae to glabrous, rarely sparsely stellate; basal veins 5(to 7), all but the inner weak; main secondary veins above base 3 to 5(6) per side, visible on abaxial surface; domatia usually present at base of larger leaves, sometimes absent, if present often well developed with a distinct roof, but no or a few straight or few-branched trichomes in association. Inflorescences 1 or 2 per node, 1- to 3(to 5)-flowered, the larger with branched peduncles; peduncle 1–5.5 mm, papillate or flat-scaly; pedicels 14–22 mm, papillate; bracteoles immediately caducous, rarely present, ca. 0.5 mm, irregularly ovate to broadly oblong, papillate; at full elongation of pedicel position of bracteole scars ranges from below midpoint of pedicel to above midpoint but well beneath flower. Sepals 5–6.5 mm, mostly not reflexed, papillate; petals 8–9.8 × 3.6–5.3 mm, obovate to elliptical, often somewhat concave, symmetrical or nearly so; corona 0.7–1.1 mm (postanthesis); stamens 15; filaments (1.2–)2.4–3.8 mm; anthers (1–)1.3–1.7 mm; staminodes linear, (2.5–)3–4 mm, usually similar in length to filaments of fertile stamens; style 3.2–4 mm, glabrous or bearing minute trichomes or papillae; style branches two, 1.5–2 mm. Fruit subglobose, somewhat vertically compressed or broadest at base, 3–4.2 mm diam., densely stellate; mature seeds not seen, only 1 ovule per fruit or possibly 1 per locule developing.

Distribution, habitat, and phenology. *Dombeya vohemarensis* is native to humid forests of extreme northern Madagascar, on sand. One collection (*Ranirison 591*) noted an elevation of 415 m. Material in flower has been collected in April and immature fruits in April and May.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya vohemarensis* is noted as Endangered or EN B2ab(iii). Fewer than five localities are known, none in protected areas, and habitat degradation is ongoing in the area.

Discussion. *Dombeya vohemarensis* is distinguished from the messy *D. subviscosa* species complex (see previous discussion) by several features, including its generally sinuate leaf margins, rather different domatia (often well developed with a pronounced roof, but less pubescent than large domatia in the latter species), larger flowers (with petals comparable in size to those of the large-flowered *D. subviscosa* subsp. *ihosyensis*, but sepals larger), sepals that are often not reflexed even in fruit, and staminodes similar in length to filaments of

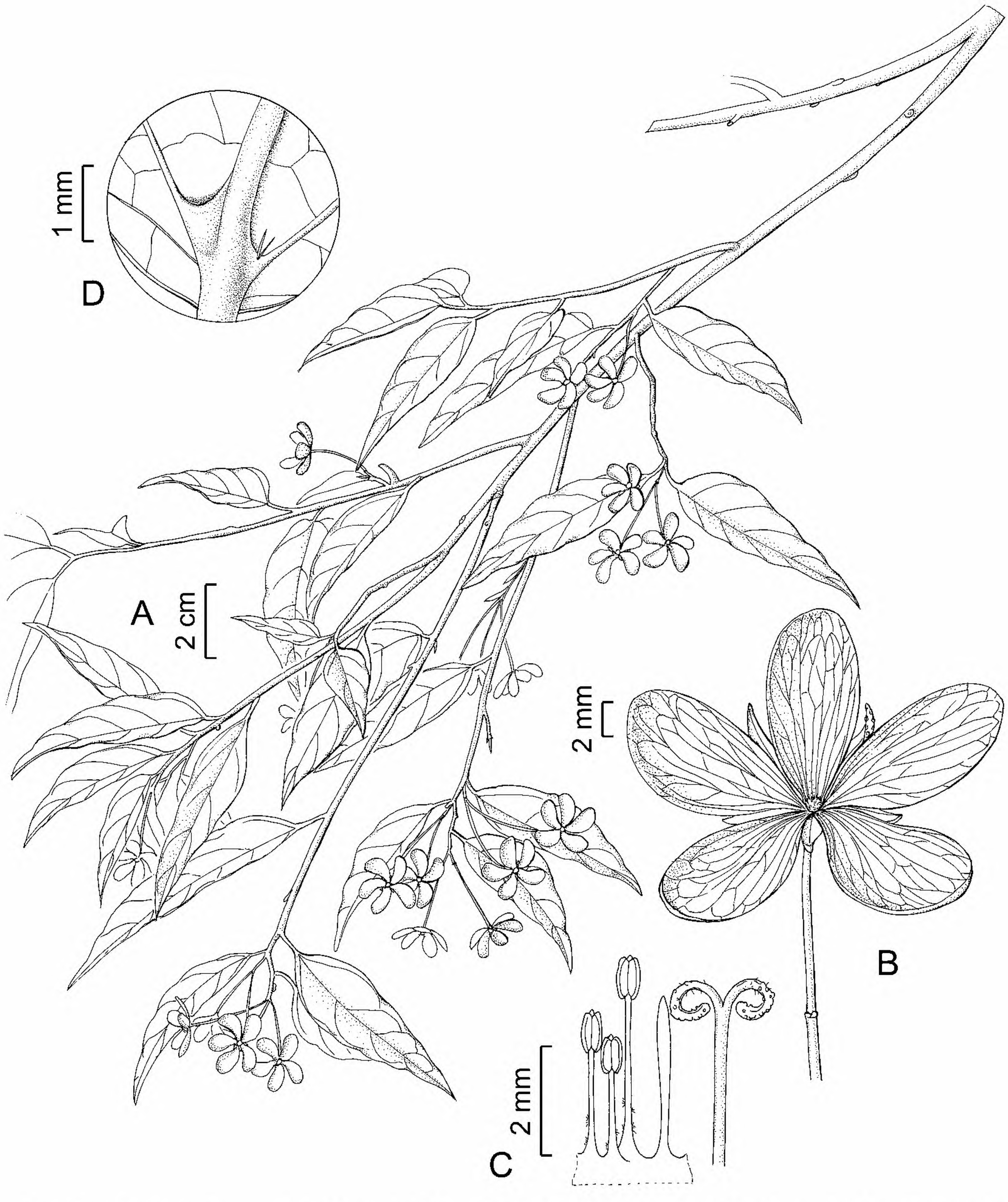


Figure 5. *Dombeya vohemarensis* Appleq. —A. Habit. —B. Corolla and calyx. —C. Androecium and style. —D. Domatia. A–D from *Rabehevitra et al. 941* (MO).

fertile stamens (rather than being conspicuously shorter as in *D. subviscosa* and other species of presumed close relationship). *Service Forestier 22702*, from a locality near Montagne des Français, is morphologically distinct from the Vohemar collections, with much broader leaves and slightly smaller flowers (which are described as "visqueuses au séchage").

Paratypes. MADAGASCAR. **Antsiranana:** sous-préfecture de Vohemar, commune rurale de Daraina, forêt d'Ampondrabe, à 630 m du point côté 594, au 97°, 12°57′47″S, 049°42′22″E, 415 m, 9 Apr. 2004 (fl., fr.), *P. Ranirison 591* (MO, P); fivondronana Vohémar, firaisana Tsarabaria, fokontany Manakana, forêt littorale d'Ambondrobe, 13°42′46″S, 50°05′25″E, 20 May 2004 (fr.), *R. Razakamalala & D. Rabehevitra 1333* (MO); bassin de la Saharaina, forêt de Sahafary, 25 Apr. 1963 (fr.), *Service Forestier 22702* (MO, P [2]).

VI. Dombeya ser. **Squamigerae** Arènes, Candollea 16: 361. 1958. TYPE: *Dombeya andrahomanensis* Arènes.

Dombeya subser. *Decaryanae* Arènes, Candollea 16: 374. 1958. TYPE: *Dombeya decaryana* Arènes.
Dombeya subsect. *Longipedicellatae* Arènes, Candollea 16: 361. 1958. TYPE: *Dombeya longipedicellata* Hochr.
Dombeya subser. *Merika* Arènes, Candollea 16: 362. 1958. TYPE: *Dombeya merika* Arènes.

Young twigs papillate, stellate, lepidote, glabrous, pilose, or scurfy; stipule scars narrow and inconspicuous or less often narrowly elliptical or narrowly crescent-shaped, then sometimes pale and somewhat prominent. Leaves elliptical to narrowly elliptical (occasionally tending to narrowly oblong-elliptical or narrowly obovate), lanceolate, or ovate (sometimes tending to rhomboid or deltoid); basal veins (1 to)5(to 7); secondary veins 3 to 9(10) or rarely numerous; domatia absent (except in *Dombeya tavia*); petioles papillate, stellate, lepidote, glabrous, or pilose. Inflorescences umbellate, few-flowered, or 1- or 2-flowered (rarely a few-flowered, usually umbelliform cyme), papillate to sparsely stellate, fimbriate-lepidote, glabrous, stellate, or partially scaly; peduncles 0.5–15(–24) mm (to 32 mm in aberrant cymose inflorescences), shorter than pedicels or rarely similar in average length. Petals broadly obovate to orbicular, obovate, or elliptical, in *D. longipedicellata* often somewhat rhomboid, near-symmetrical to strongly asymmetrical, not convex; stamens 10 to 15(to 20); staminodes ± oppositisepalous, usually longer than longest fertile filaments, rarely equal to or shorter than longest filaments; ovary stellate, glabrous, papillate, or fimbriate-lepidote.

Distribution and habitat. The species of *Dombeya* ser. *Squamigerae* occur mostly in dry forests or bush from northwestern to central and southern Madagascar at altitudes of 30–1100 m. However, two species are endemic to a high-altitude (1432–1800 m) southeastern habitat, and one, *D. merika*, is found in eastern humid forest at moderate elevations (685–900 m).

Discussion. As herein circumscribed, *Dombeya* ser. *Squamigerae* contains 11 species, including most species of Arènes' (1958) short-peduncled *Dombeya* subsect. *Longipedicellatae* that have not been placed within *Dombeya* ser. *Selinala*. As such, *Dombeya* ser. *Squamigerae* is recognized for taxonomic convenience, although it may not be monophyletic. Most of the included species have elliptical to ovate leaves, and all but one are native to relatively dry, either western to southern or high-altitudinal habitats. A plausibly natural group of five species in northwestern to central Madagascar, comprising *D. longipedicellata*, *D. pauciflora* Appleq., *D. tavia*, *D. tsiandrensis* Arènes, and *D. tubulosoviscosa* Hochr., share similar ecological conditions and morphological features. The inflorescences of most are consistently few-flowered or usually geminate, with the pedicels often dramatically longer than the pedicels, and in three species, apically thickened. The affinities of the other included species are less obvious. *Dombeya lecomtei*, with its narrowly lanceolate leaves and distinctive floral morphology, is the most problematic. It is in most ways distinct from the other species included in this series (except that it shares the very rare character of sharply bent pedicels with *D. lecomteopsis* Arènes) and is left here only to avoid describing a new series for it. All of the species included in this series, except *D. lecomtei*, are known from very few collections and appear to be rare.

Dombeya andrahomanensis was segregated by Arènes (1958) as the only species of *Dombeya* ser. *Squamigerae* because of its lepidote ovary, but this is a weak basis for the circumscription of a series, given the variability of indument in *Dombeya*. It may be conveniently treated with the other species herein included in this series because of its leaf shape and usually narrow stipule scars, short peduncles, and occurrence in dry habitats; however, it might also have affinities to *D. capuroniana* within *Dombeya* ser. *Mananarenses*. As no other series-level names were typified by members of this group, *Dombeya* ser. *Squamigerae* is the name with priority, which is regrettable as *D. andrahomanensis* is not among the distinctive core species of the group and most of the included species are not lepidote, nor are they squamate.

KEY TO THE SPECIES OF *DOMBEYA* SER. *SQUAMIGERAE*

1a. Pedicels 1.5–8.5 cm, always much longer than peduncle, the distal end conically thickened; sepals not or inconsistently reflexed; ovary glabrous or papillate; northwestern Madagascar.
  2a. Inflorescences (2)3- to 7-flowered; known material with petals 6–7.5 mm, obovate, ± symmetrical; ovary papillate ..... 41. *D. tubulosoviscosa*
  2b. Inflorescences 1- to 3-flowered or usually geminate; petals variable in size and shape, usually broadly obovate and somewhat asymmetrical or else rhomboid; ovary glabrous.
    3a. Leaves ovate to somewhat rhomboid with crenate-serrate margins; flowers (1)2; pedicels minutely papillate; petals 7–9 mm ..... 40. *D. tsiandrensis*

3b. Leaves elliptical to ovate with crenulate-serrulate margins; flowers 1 to 3; pedicels glabrous; petals 11.5–17 mm ..... 35. *D. longipedicellata*

1b. Pedicels 5–26 mm, sometimes only slightly longer than or equal to peduncle, the distal end terete or sharply bent; sepals almost always reflexed; ovary stellate or fimbriate-lepidote.

4a. Twigs, petioles, and inflorescences stellate; petals (10–)11–14 mm, often reflexed in fruit; filaments slightly longer than staminodes; northwestern Madagascar ..... 39. *D. tavia*

4b. Twigs, petioles, and inflorescences papillate (sometimes also with few stellate trichomes), fimbriate-lepidote, small-scaled, or glabrous; petals usually < 10 mm (to at least 11 mm in 1 species), not known to become reflexed; filaments almost always shorter than staminodes; south central to southeastern (eastern) Madagascar.

5a. Pedicels sharply bent beneath flower; sepals at least basally papillate with tiny reddish or pale papillae.

6a. Leaves narrowly lanceolate, margins shallowly wavy to crenate-serrate or seldom crenulate to subentire; petals usually spreading open ..... 33. *D. lecomtei*

6b. Leaves narrowly elliptical to narrowly oblong-elliptical or lanceolate-elliptical, margins finely serrulate; petals broad and often open enough to reveal androecium and gynoecium, but not conspicuously spreading; Ambatofinandrahana ..... 34. *D. lecomteopsis*

5b. Pedicels not sharply bent beneath flower; sepals bearing small scurfy to flat-stellate scales or lepidote.

7a. Twigs glabrous; leaf margins serrulate; petals on type > 9 mm, staminodes 6–6.5 mm, style 4.5–7 mm; Ambatofinandrahana ..... 32. *D. decaryana*

7b. Twigs papillate or fimbriate-lepidote; leaf margins crenate-serrulate, crenate, wavy, or subentire; petals < 9 mm, staminodes to 4 mm, style < 5 mm.

8a. Twigs and petioles densely fimbriate-lepidote; leaves narrowly elliptical to narrowly oblong-elliptical ..... 31. *D. andrahomanensis*

8b. Twigs and petioles papillate, sometimes also sparsely stellate; leaves ovate to broadly ovate, ovate-deltoid, or lanceolate.

9a. Twigs and petioles papillate with pale papillae and often sparsely stellate; leaves ovate to lanceolate with acute to rounded apices ..... 38. *D. seyrigiana*

9b. Twigs and petioles often reddish papillate, without stellate trichomes; leaves ovate to broadly ovate or ovate-deltoid with acuminate apices.

10a. Leaves ovate to broadly ovate, with (3 to)5 basal veins; stamens 10; style glabrous; ovary stellate, sometimes stellate-scaly in fruit; E humid forest ..... 36. *D. merika*

10b. Leaves ovate to ovate-deltoid, with 5 to 7 basal veins; stamens 15; style sparsely short-pubescent on most of length; ovary fimbriate-lepidote to near-stellate; S central Madagascar ..... 37. *D. pauciflora*

31. Dombeya andrahomanensis Arènes, Candollea 16: 361–362. 1958. TYPE: Madagascar. Toliara: environs d'Andrahomana, distr. de Fort Dauphin, alluvions, 4 Sep. 1924 (fr.), *R. Decary 3118* (holotype, P!; isotype, P!).

Tree; twigs pale grayish brown, the youngest lepidote with a dense coating of fimbriate scales, the leaf scars on older twigs unusually prominent; stipules caducous, lanceolate, 2.5–3.5(–6) mm, lepidote; stipule scars on young twigs small, narrowly elliptical to sublinear or seldom narrowly crescent-shaped, not distinctively colored or prominent. Leaves narrowly elliptical to narrowly oblong-elliptical, 3.5–11.6 × 1–2 cm; petiole 3–11(–16) mm, lepidote; base cuneate to rounded; apex acute with rounded tip; margins subentire to shallowly sinuate, with glands located in marginal concavities, sometimes projecting slightly; both surfaces lepidote or the upper surface bearing small scurfy stellate trichomes; basal veins 1; secondary veins numerous, weak, sometimes inconspicuous on both surfaces; domatia absent. Inflorescences 2- to 5-flowered umbels or umbelliform cymes (rarely a cyme with up to 9 flowers and elongated internal branches); peduncle 4.5–8.5 mm; pedicels 5–8 mm; peduncle and pedicels lepidote, bracteoles persistent, ovate to lanceolate, 0.6–0.9 mm, lepidote, borne immediately beneath flower or almost so. Sepals 2.5–3.5 mm, often ovate, reflexed or not, lepidote; petals white, (2.5–)3–4.8 × 2–2.5(–3) mm, broadly obovate, nearly symmetrical; corona 0.8–1 mm; stamens 15; filaments 0.5–1.2 mm; anthers 0.7–0.8 mm; staminodes spatulate, 2(–2.5) mm; style 1–1.5 mm, basally lepidote; style branches two to three, 1.3–2(–2.5) mm; ovary lepidote. Developing fruit subglobose, to 2.3 mm high, 2 mm diam., pale, lepidote; apparently 1 seed developing per locule, irregularly ovoid, somewhat compressed, to at least 1.4–1.5 mm, dark brown; mature fruit possibly dispersed as a unit leaving perianth remains.

Distribution, habitat, and phenology. *Dombeya andrahomanensis* is native to dry bush in southern Madagascar. Flowering material has been collected in February and fruits, probably immature, in March and September.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya andrahomanensis* is noted as Endangered or EN B1ab(iii)+B2ab(iii). The species is known from only

two populations, neither protected from continuing habitat loss and neither recently collected.

Additional specimens examined. MADAGASCAR. **Toliara:** massif of Angavo, E of Antanimora, *Service Forestier 11716* (P [2]); Angavo, Antanimora, *Service Forestier 14012* (P).

32. Dombeya decaryana Arènes, Candollea 16: 374–375. 1958. TYPE: Madagascar. Fianarantsoa: environs d'Ambatofinandrahana, 1600–1800 m, quartzite, 21 Feb. 1938 (fl.), *R. Decary 13173* (holotype, P!; isotypes, MO!, P!).

Small tree; twigs grayish brown, glabrous; stipules rapidly caducous, 1.5–2 mm, deltoid-acuminate, glabrous; stipule scars on young twigs narrow, not prominent. Leaves elliptical to slightly ovate, 2.9–6.3 × 1.4–3 cm; petiole (2–)6–7 mm; base ± rounded, often slightly asymmetrical; apex cuspidate to acuminate; margins serrulate with glands in apices of small rounded teeth; both surfaces glabrous; basal veins 5; secondary veins above the base 4 to 6 per side, visible on adaxial surface; domatia absent. Inflorescences 1- to 4-flowered, sometimes paired; peduncle 1–5 mm, glabrous; pedicels 8–16 mm, glabrous; bracteoles caducous, ovate, 2–3.4 mm, borne immediately below flower. Sepals 5.5–7 mm, reflexed, densely scaly with small semi-stellate scales, glandular patch sometimes possibly absent; petals white, 9–11 × 5–7(–10) mm, broadly obovate to obovate or suborbicular, nearly symmetrical; corona 1.5–2.1 mm; stamens 15; filaments 2.2–4 mm, sometimes basally fused above corona; anthers 1–1.6 mm; staminodes narrowly spatulate to linear, 6–6.5 mm; style 4.5–7 mm, long-pilose for most of its length; branches two or three, 2–3 mm, sometimes coiled; ovary somewhat laterally compressed, densely stellate with sometimes flattened multibranched trichomes.

Distribution, habitat, and phenology. *Dombeya decaryana* has been collected from the quartzite massif of Ambatofinandrahana in southeastern Madagascar, at high altitude (1600–1800 m); it flowers in February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya decaryana* is noted as Critically Endangered or CR B1ab(iii)+B2ab(iii). The only known locality is unprotected and faces ongoing threats, and recent collectors have not relocated the species.

Discussion. *Dombeya decaryana* bears obvious close affinities to *D. lecomteopsis* (see discussion below), which is also endemic to Ambatofinandrahana; it lacks the bent pedicels seen in *D. lecomteopsis* and has longer filaments and staminodes and possibly broader leaves. It might be suspected of being a hybrid involving *D. lecomteopsis*, but no suitable second parent is known from the area.

33. Dombeya lecomtei Hochr., Candollea 3: 34–35. 1926. TYPE: Madagascar. Toliara: Ambovombe, 30 Apr. 1925 (fl.), *Decary 3722* (lectotype, designated by Arènes [1958: 377], P!; isolectotypes, G [2] not seen, G [2] images!, P [2]!).

Dombeya lecomtei [subsp. *lecomtei*] var. *valamainty* Arènes, Candollea 16: 377. 1958, syn. nov. TYPE: Madagascar. Toliara: RN XI [Andohahela], distr. Fort Dauphin, forêt sèche, 7 Feb. 1951 (fl.), *Reserves Naturelles 2749* (holotype, P!; isotypes, P [2]!, TEF not seen, TEF image!).

Dombeya lecomtei subsp. *trichostyla* Arènes, Candollea 16: 378. 1958, syn. nov. TYPE: Madagascar. Toliara: Ambovombe, 31 Jan. 1925 (fl.), *R. Decary 3544* (holotype, P!; isotypes, G not seen, G image!, K not seen, K image!).

Dombeya lecomtei var. *minoriflora* Hochr., Candollea 3: 35. 1926, syn. nov. TYPE: Madagascar. Toliara: Ambovombe [Androy], 18 Apr. 1924 (fl.), *R. Decary 2571* (holotype, P!; isotype, P [2]!).

Dombeya mandoavato Arènes, Candollea 16: 364. 1958, syn. nov. TYPE: Madagascar. Toliara: RN XI [Andohahela], canton Behara, distr. Androy, forêt sèche, 25 Jan. 1953 (fl.), *Reserves Naturelles 5022* (holotype, P!; isotypes, P!, TAN not seen, TAN image!).

Small tree, to 7(–10) m, 10 cm diam., or occasionally a shrub; twigs grayish brown, slender, the youngest bearing small irregularly shaped scales or flattened papillae, with many small protrusions at nodes where leaves were borne; stipules caducous or occasionally persistent, lanceolate, 1–2.2 mm, papillate; stipule scars on young twigs narrow, not prominent. Leaves lanceolate to narrowly lanceolate, (3.3–)5–12 × 1.2–2.5(–3) cm; petiole (3–)5–12(–16) mm, bearing small flattened, sometimes reddish papillae; base oblique to shallowly cordate or rounded; apex acuminate or rarely narrowly acute; margins shallowly wavy to irregularly crenate-serrate, crenulate-serrulate, or subentire, with brownish glands usually located at apices of teeth, less often elsewhere, prominent or embedded in margin; both surfaces, especially the abaxial, papillate with small flat, often reddish papillae; basal veins 5, the outer weak; secondary veins above base (3)4 to 7(to 9) per side, relatively conspicuous on adaxial surface; domatia absent. Inflorescences 1- to 3(to 5)-flowered, with flowers borne on a short, sometimes partly or completely divided peduncle or with peduncle essentially absent and pedicels emerging from leaf axils (rarely 2 flowers borne on a single pedicel as an

aberration); peduncle where present 0.5–6.5 mm, sometimes apically branched, sometimes bearing bracts or scars thereof midway along length, papillate; pedicels 5–13(–19.5) mm, usually sharply bent just below flower, papillate with often reddish papillae; bracteoles usually rapidly caducous, rarely persistent, oblong or ovate to lanceolate, 0.3–1 mm, papillate, borne immediately below flower. Sepals (2.8–)3.4–5.3(–6) mm, reflexed, papillate with often reddish papillae; petals white or occasionally cream, (4–)5.5–7.5(–10) × (2.7–)4–7.5(–8.5) mm, broadly obovate to orbicular, occasionally broader than long, moderately asymmetrical, usually spreading in pressed material exposing androecium and ovary; corona (0.6–)1–1.5(–2) mm; stamens 10(to 15); filaments cream, (0.8–)1.4–3.5(–5) mm, often irregularly fused above corona; anthers orange-brown, (0.6–)0.9–1.2 mm; staminodes narrowly spatulate, (1.8–)2.4–4 mm; style cream, (2–)3.5–5(–7) mm, glabrous or basally stellate, rarely short-pubescent basally; style branches 2 (very rarely to 4), possibly orange, 1–2 mm; ovary stellate, somewhat flattened. Fruit subglobose, somewhat vertically compressed, with persistent style base, to at least 3–4 mm diam., stellate; seeds 1 per fruit, immature seeds to 2 mm long, irregularly ellipsoid to broadly ovoid, pale brown; mature seeds not seen.

Distribution, habitat, and phenology. *Dombeya lecomtei* is native to dry forests, bush, and transitional forests in southern Madagascar; it has been reported on sand and gneiss at elevations of 30–900 m. It flowers from December to May (once each in June and August); fruits, generally immature, are collected from December to July.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya lecomtei* is noted as Least Concern or LC.

Vernacular names. Berehoka (*Humbert 12688*), mandoavato (*Reserves Naturelles 5022*, *Service Forestier 13789*), vala (*Boiteau 2543*, *Service Forestier 3430*, *12943*), valamainty (*Reserves Naturelles 2749*), valamena (*Service Forestier 5292*).

Discussion. *Dombeya lecomtei* is easily recognized by its narrow leaves, usually relatively conspicuous papillae on most parts (notably the pedicels), usually very broad and spreading petals, and densely stellate ovaries. It does not have obvious close affinities to any other species herein placed in *Dombeya* ser. *Squamigerae* and may prove to be more closely related to the hypothesized *Dombeya* ser. *Selinala* clade.

Dombeya mandoavato is herein synonymized with *D. lecomtei*. The former was described only from the holotype, which had unusually small and narrow petals (described by Arènes [1958, 1959] as obovate rather than obovate-suborbicular, leading to its placement in a different subseries). The holotype is in early flower and in less than ideal condition, but is identifiable as an aberrant individual of *D. lecomtei* from a locality where that species has often been collected. The infraspecific taxa described by Arènes (1958) are likewise not recognized. *Dombeya lecomtei* subsp. *trichostyla* (of which *D. lecomtei* var. *minoriflora* was stated to represent one extreme) was characterized by its basally hispid style, in contrast to the glabrous style of *D. lecomtei* subsp. *lecomtei*. The types of both were from the Ambovombe region; with the addition of further new collections, it is evident that not only are both character states frequent in that region, but that style pubescence also varies around Andohahela, in farther northern populations of the southeastern distribution, and around Ihosy (where, of two collections with intact styles, one is glabrous and one is hispid). This character seems to be rather more a matter of individual than populational variation, and as such, merits no recognition. *Dombeya lecomtei* var. *valamainty* was recognized on the basis of differences in leaf shape and margin; variation of this sort is, as far as can be determined, continuous.

There is an enormous range of variation in the size of the flowers, particularly the corolla, with some specimens having flowers almost twice the size of others, and this variation is geographically correlated. Specimens from near Ihosy, a disjunct northern portion of the distribution, always have large petals and long to very long (7 mm) styles. Three other specimens with petals 8–10 mm long come from the Ambovombe region; several other specimens from that region are slightly above average in size (petals 7–8 mm) but others are of modest size, and one (*Decary 2571*) has petals ranging from 4.5 to 8 mm on a single collection. Populations elsewhere in the southeast have petals almost always under 7 mm, but the distribution of the few specimens with extremely small flowers is not reliable (e.g., petals from 4.5 to 6.5 mm are seen at Bevilany, and from 5 to 7 mm at Eromo), indicating that while genetic variation in size does have some geographic structure, the extreme variants do not occur solely as isolated populations, but co-occur with more average individuals. Formal taxonomic recognition of this variation, therefore, does not seem possible at this time, although with more samples from Ihosy that variant might prove to be separable.

Additional specimens examined. MADAGASCAR. **Fianarantsoa:** Amboloandro, near Belomboany and Zazafotsy, *Perrier de la Bâthie 2186* (P); Andrandohy S of Ambinda (PK 32, rte. Ihosy–Ivohibe), *Service Forestier 22612* (P [2]); near crossroads of routes from Ihosy to Ivohibe and Iakora, *Service Forestier 22628* (P [2]). **Toliara:** Marovato, *Boiteau 2543* (P); Beraketa, *Bosser 17845* (MO, P [2]); Rte. 10, 16 km W of Manambaro, *Croat 31945A* (P); Fort Dauphin, *Debray s.n.* (P); Ambovombe, *Decary 2542* (MO, P), *2768* (P), *2993* (P [2]), *8554* (MO, P [2]), *8580* (MO, P [3]), *9076* (MO, P [2]), *9542* (P); Irakoka, E of Ambovombe, *Decary 9613* (MO [5], P); S of Betioky, *Guillaumet 2485* (P); s. loc., *Homolle 1752* (P [2]); middle valley of the Mandrare near Anadabolava, *Humbert 12688* (P [2]); mountains between Andohahela and Elakelaka, between Ampahiso and Mahamavo, *Humbert 13716* (P [3]); Mont Eromo near Beraketa, *Humbert 14176* (P), *14177* (P); along RN 13, PK449, 42 km W of Fort Dauphin, 25°01′20″S, 046°38′55″E, *Lowry et al. 5032* (MO); Ambovombe, forest 3 km E of town, 25°09′30″S, 046°08′10″E, *Phillipson & Bürki 5821* (P); Andohahela, parcelle 3, *Phillipson & Milijaona 3518* (MO, P); Anosy, Ranopiso, 1.8 km SW of Ankilivalo, *Rakotovao et al. 5485* (MO); Andohahela RNI, parcelle 3, *Randriamampionona 133* (MO, P); Andohahela, parcelle 2, *Randriambololona et al. 87* (MO, P); Sasaké, Ambovombe, *Service Forestier 3430* (P); Anjiozio, Vohimainty, Behary, *Service Forestier 5292* (MO, P [3]); massif of Angavo, E of Antanimora, *Service Forestier 11721* (P [3]); Angavo, Antanimora, Ambovombe, *Service Forestier 12943* (P [2]); Bevilany (between Amboasary and Ranopiso), *Service Forestier 18697* (P [3]); E of Ambovombe, *Service Forestier 20441* (MO, P [2]); Bevilany, E of Amboasary, *Service Forestier 20493* (MO, P); massif of Vohipary NW of Andalatunisy (Antanimora), *Service Forestier 22499* (MO, P), *22505* (MO, P [2]); massif of Vohidava near Anadabolava, *Service Forestier 22590* (MO, P).

34. Dombeya lecomteopsis Arènes, Candollea 16: 376–377. 1958. TYPE: Madagascar. Fianarantsoa: environ[s] d'Ambatofinandrahana, 1600–1800 m, quartzite, 21 Feb. 1938 (fl.), *R. Decary 13135* (holotype, P!; isotype, P!).

Tree to 10 m; twigs brown to grayish brown, the youngest minutely papillate; stipules rapidly caducous, 1.5–2 mm, deltoid-acuminate to lanceolate, sparsely papillate; stipule scars on young twigs narrow, not prominent; base convex to rounded, usually slightly asymmetrical. Leaves narrowly elliptical to narrowly oblong-elliptical to somewhat lanceolate or narrowly obovate, 4.5–9.5 × 1.5–3.3 cm; petiole 6–13 mm, sparsely papillate to glabrous; apex acuminate or occasionally rounded; margins serrulate with glands in apices of small rounded teeth; abaxial surface minutely papillate with often reddish papillae, adaxial surface sparsely papillate to glabrate; basal veins 3 to 5, all weak, often asymmetrical; secondary veins above the base 7 to 9 per side, visible on adaxial surface; domatia absent. Inflorescences (1)2- to 4-flowered, often 2(3) per node; peduncle 1–6 mm, minutely papillate, sometimes apically short-branched; pedicels 8–14 mm, usually sharply bent just below flower, minutely papillate; bracteoles rapidly caducous, narrowly oblong, ca. 1.5 mm, borne immediately below flower and leaving a prominent fluted scar on the side of the receptacle opposite the pedicel. Sepals 5–6 mm, reflexed, minutely papillate at least at base; petals white, 8.6–10 × 5.5–10 mm, broadly obovate to obovate or suborbicular, slightly to moderately or less often strongly asymmetrical; corona 2–3 mm; stamens 15 to 20; filaments white, 0.7–2(–2.5) mm; anthers 1.6–2 mm; staminodes narrowly spatulate, 2.8–4 mm; style 4–5.3 mm, pilose or at least bearing a few straight trichomes near base; branches 2, white, 2–2.5 mm, coiled; ovary somewhat laterally compressed, densely stellate, containing globules of gelatinous matter.

Distribution, habitat, and phenology. *Dombeya lecomteopsis* has been collected from the quartzite massif of Ambatofinandrahana in southeastern Madagascar, in dry forest at high altitude (1432–1800 m); it flowers in February and March.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya lecomteopsis* is noted as Critically Endangered or CR B1ab(iii)+B2ab(iii). The only known locality is unprotected and faces ongoing threats; label data from the most recent collection (*Skema 52*) noted that the plant was found in a forest relic bordered by cultivated land and savannahs.

Discussion. *Dombeya decaryana* and *D. lecomteopsis* were described by Arènes (1958) from two Decary collections made around Ambatofinandrahana (a seldom collected locality) on the same day. The two share similar morphology, including both general appearance and unusual derived characters such as a long-pubescent style, and are undoubtedly closely related. *Dombeya lecomteopsis* has bent pedicels like those of *D. lecomtei*, suggesting a close relationship to that species as well, while *D. decaryana* does not. The androecium and gynoecium of *D. lecomteopsis* are smaller than those of *D. decaryana* except for longer anthers (in particular, the staminodes are 2.8–4 mm vs. 6–6.5 mm), and the sepals bear minute papillae rather than scurfy-stellate scales. Leaves of *D. lecomteopsis* may be somewhat narrower and have more secondary veins. The possibility that *D. lecomteopsis* represents a first-generation hybrid of *D. decaryana* × *D. lecomtei* is rejected because *D. lecomtei* is not known from the area nor known to occur above 900 m, and because the second collection now identified as *D. lecomteopsis* is morphologically very consistent with the type.

Additional specimens examined. MADAGASCAR. **Toliara:** Amoron'i Mania, 7 km NNE of Ambatofinandrahana village, *Skema 52* (MO [2]).

35. Dombeya longipedicellata Hochr., Candollea 3: 32–33. 1926, as "*longepedicellata*." TYPE: Madagascar. Mahajanga: rocailles calcaires et boisées de Vilanandro près d'Andranomavo (Ambongo), Aug. 1905 (fl.), *H. Perrier de la Bâthie 5516* (holotype, G not seen, G image!; isotype, P!).

Shrub, to at least 4 m, or tree; twigs grayish brown, the youngest stellate with small thin trichomes or pilose; stipules caducous, linear to very narrowly deltoid, 2.5–4(–8) mm, sparsely pubescent; stipule scars on young twigs very narrowly elliptical, pale, not prominent. Leaves elliptical to ovate, 5.5–13.5 × 2.4–6 cm; petiole 2–5 mm, thin-stellate or pilose; base ± rounded or rarely shallowly cordate; apex acuminate or rarely cuspidate or acute; margins irregularly crenulate to serrulate with inconspicuous glands variably located in tooth apices or between teeth; both surfaces sparsely small-stellate or more densely pilose, at least along veins; basal veins 5(rarely 7); secondary veins above the base 5 to 9 per side, inconspicuous on adaxial surface; domatia absent. Inflorescences 1- to 3-flowered; peduncle 3–15(–23) mm, glabrate with a few small stellate trichomes; pedicels (4–)5–7(–8.5) cm, glabrous; bracteoles very early caducous, linear, 1.5 mm, glabrate; at anthesis uppermost part of pedicel thickened, at least one bracteole scar slightly below flower, bracteole scars not all at the same level. Sepals 6.2–7.5(–11.5) mm, narrow, not reflexed, glabrous; petals white, at least sometimes purplish red at the base, 11.5–17 × 7.5–11.5 mm, broadly obovate, usually asymmetrically, or somewhat rhomboid with rounded apex and symmetrical; corona 1.5–3 mm; stamens 10 to 15; filaments (0.5–)1.5–3 mm; anthers 1.4–2.1 mm; staminodes linear, 3–6 mm; style 5–9 mm; style branches two, 1–1.5 mm; ovary glabrous. Immature fruit subglobose, to at least 3.3 mm diam., dark brown, wrinkled; mature fruit not seen.

Distribution, habitat, and phenology. *Dombeya longipedicellata* is native to dry forests of northwestern Madagascar on limestone. It flowers from August through December; immature fruit has been collected in December.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya longipedicellata* is noted as Endangered or EN B1ab(iii)-2ab(iii). Fewer than five historical populations are known, there have been no recent collections, and potential habitat is almost all unprotected and subject to continuing degradation.

Vernacular name. Mabolotsaky (*Reserves Naturelles 11445*).

Discussion. *Dombeya longipedicellata* displays unusual variability in pubescence: most specimens have a modest indument of thin stellate trichomes on most parts of the plant, whereas two have a somewhat heavier coating of long unbranched trichomes mixed with few stellate trichomes, a type of pubescence that is very unusual in this group. These specimens include one of the two fragments on the type sheet and one other collection from Andranomavo. Because this variation apparently occurs or did occur within a single population and is not consistently correlated with variation in other morphological characters, formal taxonomic recognition would be inappropriate.

Hochreutiner (1926) published this species as *Dombeya longepedicellata*; the use of an inappropriate compounding form is treated as an error to be corrected (Art. 60.8 of the ICN; McNeill et al., 2012). Arènes (1958) declared the duplicate of the only cited collection, *Perrier de la Bâthie 5516*, at P to be the lectotype, but the duplicate at G should be considered to be the holotype. Hochreutiner did not indicate that the specimen he saw came from another herbarium (see discussion under *D. aquifoliopsis*), and the quoted label data did include the words "de Vilanandro," which are omitted from the P duplicate's label, demonstrating that Hochreutiner had used the G duplicate.

Leaves are usually small and not fully mature at anthesis and have been reported to be caducous (*Perrier de la Bâthie 17831*). The wood is reported to be hard and used for construction (*Reserves Naturelles 7742*).

Additional specimens examined. MADAGASCAR. **Mahajanga:** Namoroka (Ambongo), *Perrier de la Bâthie 17831* (P); s. loc., s.d., *Petit s.n.* (P); Andranomavo, Soalala, *Reserves Naturelles 6858* (P); Ankoakibe, Andranomavo, Soalala, *Reserves Naturelles 7742* (MO, P [3]), *11445* (P [2]).

36. Dombeya merika Arènes, Candollea 16: 362–363. 1958. TYPE: Madagascar. Toamasina: forêt d'Ambodiala, à 7 km au S d'Andilamena, 685 m, 8 May 1942 (fl., fr.), *G. Cours 1663* (holotype, P!; isotypes, P!, TAN not seen, TAN image!).

Dombeya coursii Arènes, Candollea 16: 375–376. 1958, syn. nov. TYPE: Madagascar. Toamasina: distr. d'Ambatondrazaka, s.d. (fl.), *Cours 275* (holotype, P!; isotype, P!).

Tree to 20 m, to 30 cm diam.; twigs grayish or reddish brown, the youngest bearing minute flattened, sometimes reddish papillae; stipules caducous, ca. 1 mm, possibly ovate, papillate to glabrate; stipule scars on young twigs narrow, not prominent. Leaves ovate to broadly ovate, 3.5–8.6 × 2–3.8(–4.3) cm; petiole (4–) 6–11 mm, papillate; base rounded to shallowly cordate; apex acuminate; margins irregularly crenulate or shallowly wavy to subentire, with glands borne in concave portions, usually sunken, occasionally prominent; both surfaces sparsely flat-papillate, especially along veins, to glabrous; basal veins (3 to)5; secondary veins above base (3)4 to 8 per side, variably curving or nearly straight, sometimes apparently craspedodromous, in mature leaves sometimes not visible on adaxial surface; domatia absent. Inflorescences 1- to 3(to 7)-flowered, occasionally a 4-flowered umbelliform cyme, rarely a several-flowered cyme with elongated internal branches; peduncle 0.5–11 mm, papillate to glabrate; pedicels 9–19(–25) mm, papillate, sometimes scaly stellate on uppermost portion above attachment of bracteoles; bracteoles very rapidly caducous, not seen, the scars at anthesis well below flower. Sepals 3.2–5.3 mm, reflexed, scurfy to scaly stellate; petals white, (4.5–)6–8.2 × (2.6–)4–5(–6) mm, broadly obovate to elliptical, ± asymmetrical; corona (1–)1.3–1.8(–2.8) mm, at least somewhat narrowed above ovary and occasionally reflexed; stamens 10; filaments white, 0.8–2.4 (–3) mm, sometimes irregularly fused above corona; anthers rust colored or yellow, 0.7–1.1 mm; staminodes narrowly spatulate, 2.5–3.5 mm; style (2.5–)3.5–4.7 mm; style branches 2(3), green, 1–1.5 mm, spreading; ovary stellate. Fruit subglobose, slightly laterally compressed, 2.5–3.2 mm diam., dark or pale brown with sparse stellate or stellate-scaly indument; immature seeds 1 per fruit, dark brown, irregularly shaped and very deeply wrinkled, but not significantly compressed; mature seeds not seen.

Distribution, habitat, and phenology. *Dombeya merika* is primarily native to humid forests of eastern Madagascar, at elevations of 685–900 m; it has been reported to occur on sandy soil and along riverbanks. One collection reportedly comes from the western region of Ambohijanahary, on the border between Mahajanga and Toliara provinces; as forest in that area would be much drier, this location seems suspicious and should be further investigated if possible. It flowers from April to August; immature fruit has been collected from May to August.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya merika* is noted as Vulnerable or VU, D. Most of the five known locations are close together and vulnerable to stochastic events, though some are protected.

Vernacular names. Hafotra merika (*Service Forestier 3531, 16877*), merika (*Service Forestier 26789*).

Discussion. The type of *Dombeya coursii* has larger leaves than other existing collections but is clearly conspecific with *D. merika*; the leaf morphology is distinctive enough to distinguish this species from most others. The two names have equal priority; *D. merika* is preferred because its type, though unusually small flowered, is in better condition and has better locality data, and *D. merika* has been the name more commonly used in the herbarium.

The wood is used for construction (*Service Forestier 26789*).

Additional specimens examined. MADAGASCAR. **Toamasina:** NE of Moramanga, *McPherson 17148* (MO); Antsahatsaka, Périnet, *Service Forestier 3531* (P); Antamiditra, Périnet, Moramanga, *Service Forestier 16877* (MO, P); Andranomandry, Moramanga, *Service Forestier 26789* (P). **Unknown locality:** forest of Ankitsika, canton of Ambohijanahary, *Cours* [*Herb. Inst. Sci. Mad.*] *1585* (MO, P [2]); s. loc., *Keraudren 1147* (P).

37. Dombeya pauciflora Appleq., sp. nov. TYPE: Madagascar. Fianarantsoa: berges de la rivière Ilempona, à 6 km à l'W d'Ihosy à la base du plateau de l'Horombe, 23 Feb. 1970 (fl.), *Service Forestier 29075* (holotype, P!; isotype, P!). Figure 6.

Diagnosis. Differs from *Dombeya tsiandrensis* Arènes in having often ovate-deltoid leaves with broader base, consistently acuminate apex; sparsely and minutely papillate indument on the twigs, petioles, leaves and peduncles; sepals fimbriate-lepidote, reflexed; ovary fimbriate-lepidote to nearly stellate.

Small tree, to 5–6 m; twigs grayish brown, the youngest sparsely papillate with minute flat reddish papillae; stipules caducous, lanceolate, (1.6–)2.9–3.2 mm, papillate; stipule scars on young twigs narrow, not prominent. Leaves ovate to ovate-deltoid, (2.8–)3.5–5.5 × 1.9–3 cm; petiole (4.5–) 7–12 mm, reddish papillate; base shallowly cordate, broad with sometimes nearly rounded-truncate appearance; apex acuminate; margins irregularly crenate, with teeth often shallow, occasionally large and rounded, or shallowly wavy, with glands borne in apices of teeth or in concavities between teeth; both surfaces at least sparsely papillate with minute flat reddish papillae; basal veins 5 to 7, the outermost weak; secondary veins above the base 3(4) per side, visible on adaxial surface; domatia absent. Inflorescences 1- or 2-flowered; peduncle

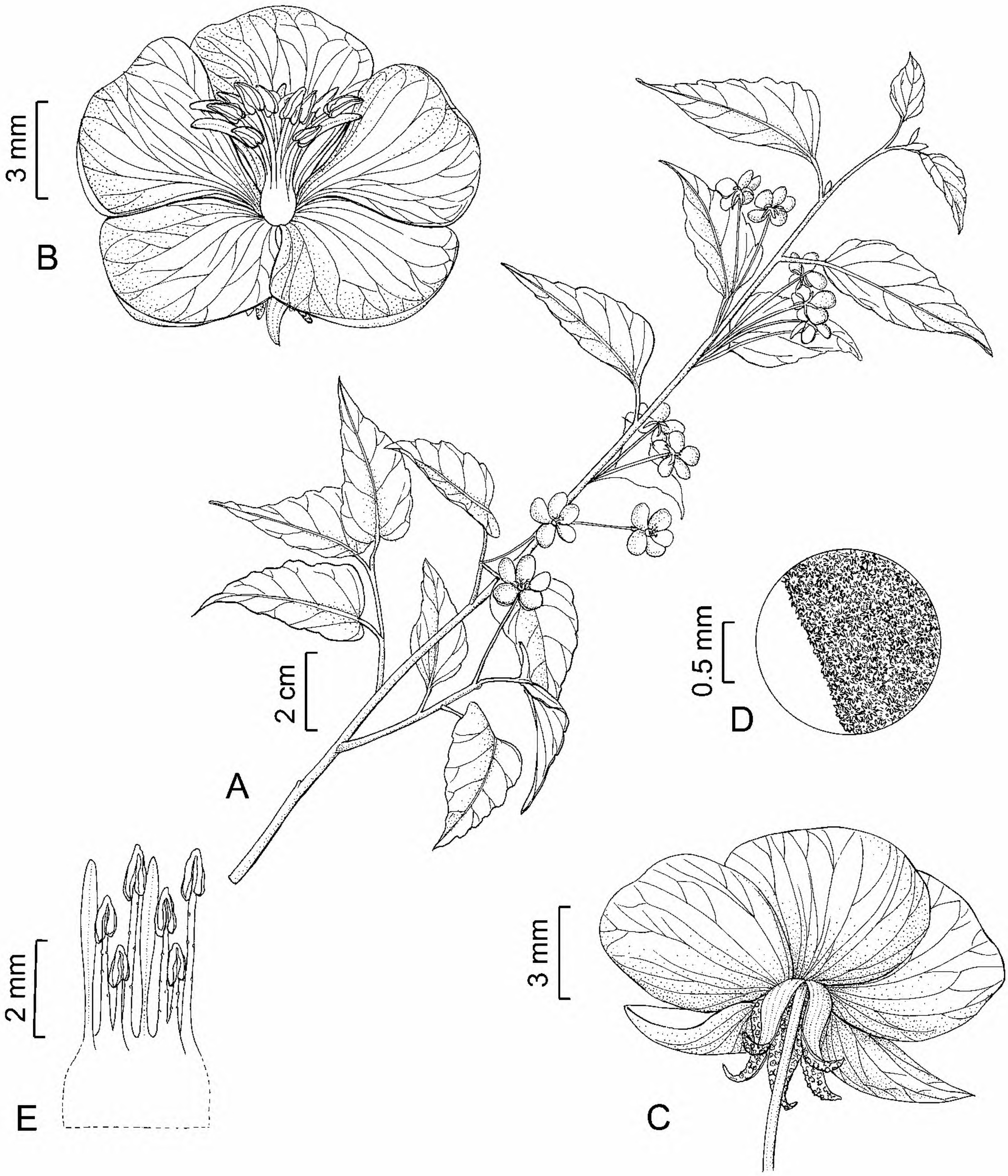


Figure 6. *Dombeya pauciflora* Appleq. —A. Habit. B–C. Flower. —D. Indument of abaxial sepal surface. —E. Androecium. A–E from *Service Forestier 29075* (P).

5.5–12.5 mm; pedicels 1.9–2.6 cm; peduncle and pedicels bearing minute, often reddish flattened papillae, the pedicels above the bracteole scars bearing scaly indument like that of sepals; bracteoles very rapidly caducous, broadly elliptical and enclosing young buds, ca. 1.5 mm, papillate; bracteole scars at maturity somewhat below flower. Sepals 4–5 mm, reflexed, with small raised irregularly fimbriate scales; petals 6–7 × 5.4–6.5 mm, suborbicular, slightly asymmetrical; corona 1–1.5 mm; stamens 15; filaments 1.5–3 mm, partly fused above corona; anthers 0.8 mm; staminodes spatulate, 3.5–4 mm; style 4.5 mm, with few small straight white trichomes over most of length; branches 2, 1 mm; ovary lepidote to semi-stellate, with an indument of small flat-stellate scales. Developing ovary subglobose, to at least 2.4 mm diam., lepidote; mature fruit not seen.

Distribution, habitat, and phenology. *Dombeya pauciflora* has been collected from a single locality in southern Madagascar, on a riverbank near Ihosy; it flowers in February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya pauciflora* is noted as Critically Endangered or CR B1ab(iii)-2ab(iii). The type locality is not protected and has suffered severe habitat degradation; although the area is quite accessible, no more recent collections have been made.

Discussion. Superficially, *Dombeya pauciflora* most resembles *D. tsiandrensis*, which has a similar general appearance and usually geminate, long-pedicelled inflorescences. However, it is distinguished from that species by details of leaf shape and floral morphology and by differences in the indument on all parts. Although *D. tsiandrensis* is somewhat stellate on the twigs, leaves, and peduncles but has papillate sepals and a glabrous ovary, *D. pauciflora* has papillate indument on the twigs, leaves, and peduncles but fimbriate-lepidote indument on the sepals and ovary. It also lacks a derived character shared among *D. tsiandrensis* and two similar northwestern species, prominent apical thickening of the pedicel. Although only one specimen is known, it can be confidently identified as a new taxon and not a hybrid, because its locality is far to the south of the only known historical population of *D. tsiandrensis*.

This species' true affinities might be with *Dombeya merika*, the only species of this group that is native to eastern humid forests in Madagascar, which does not share the character of thickened pedicels. The leaves of *D. merika* have only (three to) five rather than five to seven basal veins and do not tend to be deltoid ovate nor ever have large prominent marginal teeth; *D. merika* has only 10 stamens and a glabrous style, and its ovary is generally stellate at anthesis, though taking on a flat-stellate appearance in fruit.

The epithet of *Dombeya pauciflora* reflects the fact that the inflorescences are consistently 1- or 2-flowered. It is unrelated to Arènes' (1958) *Dombeya* subser. *Pauciflorae*, a subgroup within *Dombeya* subg. *Dombeya*, which was not derived from a validly published specific epithet within that subgroup and, lacking citation of a type species, was not validly published, as was the case for a number of Arènes' infrageneric groups, as previously noted.

38. Dombeya seyrigiana Arènes, Candollea 16: 394. 1958. TYPE: Madagascar. Toliara: Ampandrandava, crêtes à l'Est, entre Bekily et Tsivory, vers 1100 m, Apr. 1943 (fr.), *A. Seyrig 616* (holotype, P!; isotype, P!).

Small tree or shrub; twigs grayish brown, young twigs papillate with occasional small stellate trichomes; stipules caducous, lanceolate to linear, 2–3.5 mm; stipule scars on young twigs narrow, not prominent. Leaves ovate to lanceolate, 3.5–8.2 × 1.8–3.6 cm; petiole 3–8(–16) mm, usually papillate, with occasional stellate trichomes; base rounded to very shallowly cordate; apex acute or rarely rounded; margins irregularly crenate to crenulate-serrulate, with glands in tooth apices or on apical margins of teeth or between teeth; abaxial surface sparsely papillate, often with few small stellate trichomes along main veins; adaxial surface glabrous or glabrate, with rare single stellate trichomes; basal veins 5(rarely 3), the outermost weak; secondary veins above the base 4 to 7 per side, tending to craspedodromous, inconspicuous but visible on adaxial surface; domatia absent. Inflorescences 1- to 6-flowered; peduncle 6–14(–24) mm; pedicels 7–13 mm, sometimes about equal to peduncle in length; peduncle and pedicels usually inconspicuously papillate, often with few small stellate trichomes; bracteoles caducous, linear to narrowly lanceolate, (1.5–)3.5–4 mm, papillate, borne immediately below flower. Sepals 3.6–4.8 mm, usually reflexed after anthesis, with scurfy indument; petals white, 6–8 × (4–)5.5–7 mm, broadly obovate, conspicuously asymmetrical; corona 0.8–1.3 mm; stamens 15; filaments 0.5–1.5 mm; anthers 0.8–1 mm; staminodes narrowly spatulate to sublinear, 2–3.5 mm; style 2.5–3.5 mm; branches two, 1–1.5(–2.5) mm; ovary stellate. Fruit subglobose, to 4 mm diam., reddish brown, sparsely stellate; seeds 2 per fruit, apparently only 1 developing, irregularly elliptical, slightly laterally compressed, to at least 2.3 × 2 mm, dark reddish brown.

Distribution, habitat, and phenology. *Dombeya seyrigiana* is native to dry areas in southern Madagascar; it occurs on gneiss at reported altitudes of 800–1100 m. Flowers and possibly immature fruits have been collected in April.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya seyrigiana* is noted as Endangered or EN B1ab(iii)+2ab(iii). It is known from only two localities, neither protected, and has not been relocated in several decades despite more recent botanical collections of remaining natural vegetation in the regions where it was known to occur.

Discussion. *Dombeya seyrigiana*, which has peduncles equaling or exceeding the pedicels, was placed by Arènes (1958) within *Dombeya* subsect. *Decantherae*; however, its vegetative morphology and ecological preferences seem to place it more plausibly within this otherwise short-peduncled series.

Additional specimens examined. MADAGASCAR. **Toliara:** Mont Eromo near Beraketa, *Humbert 14187* (P); Ampandrandava between Bekily and Tsivory, *Seyrig 616B* (P [2]).

39. Dombeya tavia Arènes, Candollea 16: 368–369. 1958. TYPE: Madagascar. Mahajanga: Andakana, Maevatanana, 27 Jan. 1951 (fr.), *Service Forestier 3960* (holotype, P!; isotypes, MO!, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Woody plant; twigs grayish brown, the youngest at least sparsely stellate-pubescent; stipules not seen; stipule scars on young twigs narrow, not prominent. Leaves lanceolate to ovate, 5.5–10.5 × 2.5–4.3 cm; petiole 6–12(–16) mm, stellate; base rounded to cuneate and rounded at the very base; apex acuminate; margins shallowly serrate, bearing small rounded projections in which glands are located, occasionally also irregularly dentate; abaxial surface sparsely stellate-pubescent, adaxial surface sparsely stellate-pubescent, mostly along midrib, or bearing sparse minute papillae or glabrous; basal veins 5, the outermost weak; secondary veins above the base 5 or 6 per side, tending to craspedodromous (sometimes terminating in notches between teeth, especially apically), visible on adaxial surface; domatia present both basally and in juncture of some secondary veins with midrib above the base. Inflorescences few-flowered, usually only 1 flower per inflorescence developing fruit, sometimes 3-branched at base so barely cymose; peduncle 1–3 mm; pedicels 12–20 mm; peduncle and pedicels stellate; bracteoles not seen, bracteole scars close to flower. Sepals 7–8 mm, reflexed, stellate, usually persistent in fruit; petals (10–)11–14 × (4.5–)6–8 mm, obovate, cuneate with broad base, nearly symmetrical, often somewhat reflexed in fruit but usually not to an extreme degree; corona 3 mm, possibly narrowed above ovary in flower; stamens 15; filaments 6.5–7 mm; anthers 1.2–1.3 mm; staminodes linear, 6 mm; ovary stellate. Immature fruit subglobose, to 6 mm diam., dark with whitish persistent indument; seed to at least 3 mm, elliptical, dark brown, glossy, possibly only 1 per fruit developing.

Distribution and habitat. *Dombeya tavia* is native to the vicinity of Andakana, south of Maevatanana in northwestern Madagascar, presumably in dry forest.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya tavia* is noted as Data Deficient or DD. The habitat is unprotected and subject to ongoing degradation, and no re-collections have been made; it may be critically endangered. However, it is not entirely certain that *D. tavia* is a distinct species (see discussion below).

Vernacular name. Tavia.

Discussion. Within the apparently cohesive but very poorly collected group of northwestern to north-central species of *Dombeya* ser. *Squamigerae*, *D. tavia* is remarkable for having domatia in the axils of basal and secondary leaf veins (domatia being otherwise unknown in this series), very long filaments that slightly exceed the also long staminodes in length and petals that are often somewhat reflexed in fruit. Potentially, the type of *D. tavia* could represent a hybrid of *D. longipedicellata* (the only known large-flowered potential parent) × *D. subviscosa* (a common species in the region that usually has domatia, sometimes multiple pairs, and stamens that are longer than the staminodes). Both putative parents usually have at least slightly longer peduncles, and neither has reflexed petals, although hybridization involving a concave-petalled parent perhaps could result in irregularly reflexed petals. *Dombeya subviscosa* has stellate ovaries (at least post-anthesis) and occasionally stellate inflorescences, although normally never stellate sepals. However, *D. longipedicellata* has a limited known range and has never been collected in the vicinity of the type of *D. tavia*. Furthermore, known collections of *D. longipedicellata* flowered from August, perhaps atypically, through December, while *D. subviscosa* normally flowers from January to May. This phenological difference might make hybridization less likely. Lacking adequate material of this group to clarify species boundaries, continued tentative recognition of previously described taxa of uncertain status is the most conservative approach.

40. Dombeya tsiandrensis Arènes, Candollea 16: 382–383. 1958. TYPE: Madagascar. Mahajanga: plateau de Bemaraha, forêt de Behandrao, au S de Tsiandro, restes de forêt à feuilles caduques sur buttes calcaires, 500–600 m, 29 Nov. 1952 (fl.), *R. Capuron, J. Leandri & A. Razafindrakoto 1980* (*Service Forestier 6765*) (holotype, P!; isotypes, MO [3]!, P!, TAN not seen, TAN image!, TEF not seen, TEF image!).

Small tree, to 7 m, 15 cm diam., or possibly large shrub; twigs dark brown, the youngest stellate-pubescent with lax white trichomes; stipules caducous, lanceolate-acuminate to sublinear, 2–4.5 mm,

sparsely stellate; stipule scars on young twigs linear to slightly broadened, often pale and modestly prominent, often subtended by tufts of stellate trichomes. Leaves ovate, occasionally somewhat rhomboid, (3–) 5–8.8 × 2–3.5 cm; petiole 3–6 mm, at least sparsely stellate; base rounded; apex acuminate to acute with a rounded tip; margins crenate-serrate with large rounded teeth; abaxial surface sparsely stellate-pubescent, with scattered trichomes mostly along main veins; adaxial surface glabrous or glabrate; basal veins 5; secondary veins above the base 3 or 4 per side, pale and relatively weak but visible on adaxial surface; domatia absent. Inflorescences (1)2-flowered; peduncle 1.6–4(–5.5) mm, sparsely stellate; pedicels (3.6–)5.5–8.5 cm, bearing minute, often reddish flattened papillae; bracteoles caducous, ovate, thick, 0.5–1 mm, bracteole scars at anthesis prominent, borne somewhat below flower with the uppermost part of the pedicel thickened conically. Sepals 4–4.7 mm, not reflexed, glabrate with minute papillae beneath, rare single stellate trichomes; petals white, 7–9 × 5.7–7 mm, broadly obovate to suborbicular, moderately asymmetrical; corona 2.5–3 mm; stamens 15; filaments 0.5–1.5 mm; anthers 1 mm; staminodes linear, 3–4 mm; style 5–5.5 mm; branches two, 1.2–1.5 mm; ovary glabrous.

Distribution, habitat, and phenology. *Dombeya tsiandrensis* is native to dry forest on limestone near Tsiandro in northwestern Madagascar, at 500–600 m; flowering material was collected in November.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya tsiandrensis* is noted as Critically Endangered or CR B1ab(iii)-2ab(iii). The species is native to unprotected and badly degraded northwestern habitat, and it has not been relocated by more recent collectors in that region.

Discussion. The type of *Dombeya tsiandrensis* is numbered on four duplicates in Leandri's collector series, rather than Capuron's, but Capuron (who was also collecting for Service Forestier) is indicated on Leandri's printed labels as the first collector.

41. Dombeya tubulosoviscosa Hochr., Candollea 3: 37–38. 1926. TYPE: Madagascar. Mahajanga: environs de la baie de Bombetoka, bois rocailleux (calcaire), [Dec. 1907] (fl.), *H. Perrier de la Bâthie 12165* [*H. L. Jumelle 45*] (lectotype, designated by Arènes [1958: 388], P!; isolectotypes, G not seen, G image!, K [2] not seen, K [2] images!).

Dombeya majungensis Arènes, Candollea 16: 383–384. 1958, syn. nov. TYPE: Madagascar. Mahajanga: environs de Majunga, 2–15 m, restes de forêts, sur calcaire, 28–30 Dec. 1924 (fl.), *H. Humbert 4090* (holotype, P!; isotype, P!).

Sarmentose shrub; twigs grayish brown, young twigs brown, sparsely reddish stellate; stipules caducous, lanceolate-acuminate, 2–3.5 mm, sparsely stellate to glabrate; stipule scars on young twigs narrow, not prominent. Leaves elliptical to ovate or lanceolate, 4–10.5 × 1.7–3.9 cm; petiole 4–9 mm, stellate; base rounded; apex acuminate; margins crenulate to crenulate-serrulate, with glands variously located in or distally to teeth apices; abaxial surface sparsely stellate, especially along veins, or rarely glabrous; adaxial surface glabrate or glabrous to sparsely stellate; basal veins 5 or occasionally 7 with the outermost very weak; main secondary veins above base 6 to 10 or more, sometimes scarcely distinguished from interspersed smaller veins, visible on adaxial surface; domatia absent. Inflorescences (2)3- to 7-flowered; peduncle 0.5–1.5(–3) mm, sparsely stellate; pedicels 1.5–3.8 cm, glabrous; bracteoles caducous, not seen, bracteole scars slightly or rarely immediately below flower with the uppermost part of the pedicel strongly thickened. Sepals 3.5–4 mm, variably reflexed or not; petals white, 6–7.5 × 4–4.8 mm, obovate, symmetrical; corona 2–2.4 mm; stamens 15; filaments 0.8–2 mm; anthers 1–1.2 mm; staminodes 1.8–2.8 mm; style 4–5.5 mm; branches two, 1 mm; ovary flattened, papillate. Fruit subglobose, to 3 mm diam., dark brown, minutely papillose; 1 seed per fruit maturing, broadly ellipsoid to 2.8 mm with deep irregular wrinkles, dark reddish brown with minutely striated surface.

Distribution, habitat, and phenology. *Dombeya tubulosoviscosa* is native to dry forests of northwestern Madagascar, on limestone; it is known to flower in December and fruit in February.

IUCN Red List category. Preliminary IUCN Red List category (IUCN, 2001) for *Dombeya tubulosoviscosa* is noted as Endangered or EN B1ab(iii)-2ab(iii). Two historical localities are known, neither protected and both subject to anthropogenic degradation; as for other northwestern species in this series, no recent collections have been made despite the accessibility of much of the remaining potential habitat.

Discussion. Hochreutiner (1926) cited two collections of *Dombeya tubulosoviscosa*, *Perrier de la Bâthie 1240* and *Jumelle 45* from Hb. Perrier de la Bâthie (which is also numbered on most herbarium

labels as *Perrier de la Bâthie 12165*). Arènes (1958) incorrectly described the former as a paratype and the P duplicate of the latter as the holotype; however, this is a correctable error under Article 9.9 of the ICN (McNeill et al., 2012), and Arènes thus lectotypified the name. As for some other taxa (see discussion under *D. aquifoliopsis*), Hochreutiner appeared to cite only the G duplicates of the syntypes (for *Jumelle 45*, this is determined by the omission of some label data from other duplicates as well as the failure to mention any other herbarium). Article 9.12 of the ICN implies that a cited syntype should have been chosen as lectotype in preference to an isosyntype but does not make this entirely unambiguous.

The type of *Dombeya majungensis* is an immature specimen of *D. tubulosoviscosa* that has small flowers in poor condition (hence, most measurements were excluded) and small leaves.

Additional specimens examined. MADAGASCAR. **Mahajanga:** Amboranio, near Majunga, *Perrier de la Bâthie 1240* (P).

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Appendix 1. List of Accepted Names.

1. *Dombeya apikyensis* Arènes
2. *D. aquifoliopsis* Hochr.
3. *D. midongyensis* Arènes
4. *D. ramiovensis* (Arènes) Appleq.
5. *D. decanthera* Cav.

5a. *D. decanthera* Cav. subsp. *decanthera*

5b. *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.

5c. *D. decanthera* Cav. subsp. *latipetala* (Arènes) Appleq.

6. *D. lavasoensis* Arènes
7. *D. pilosissima* Appleq. & T. Andriam.
8. *D. australis* Scott-Elliot

8a. *D. australis* Scott-Elliot subsp. *australis*

8b. *D. australis* Scott-Elliot subsp. *grandiflora* Arènes

9. *D. capuroniana* Arènes
10. *D. mananarensis* Arènes
11. *D. mandenensis* Arènes
12. *D. mangorensis* Arènes
13. *D. ranofotsyensis* Arènes
14. *D. rariflora* Arènes
15. *D. gautieri* Dorr & Skema
16. *D. milleri* Appleq. & Bosser
17. *D. ratovosonii* Appleq. & Bosser
18. *D. ambalabeensis* Arènes

18a. *D. ambalabeensis* Arènes subsp. *ambalabeensis*

18b. *D. ambalabeensis* Arènes subsp. *ambongensis*

18c. *D. ambalabeensis* Arènes subsp. *analavelonae* (Arènes) Appleq.

19. *D. ambohitrensis* Arènes
20. *D. anakaensis* Arènes
21. *D. danguyi* Hochr.
22. *D. digyna* Hochr.
23. *D. micrantha* Appleq.
24. *D. parvipetala* Arènes
25. *D. sakamaliensis* Arènes
26. *D. selinala* Arènes
27. *D. sely* Arènes
28. *D. subviscosa* Hochr.

28a. *D. subviscosa* Hochr. subsp. *subviscosa*

28b. *D. subviscosa* Hochr. subsp. *ihosyensis* (Arènes) Appleq.

28c. *D. subviscosa* Hochr. subsp. *sakarahae* (Arènes) Appleq.
29. *D. tulearensis* Arènes
30. *D. vohemarensis* Appleq.
31. *D. andrahomanensis* Arènes
32. *D. decaryana* Arènes
33. *D. lecomtei* Hochr.
34. *D. lecomteopsis* Arènes
35. *D. longipedicellata* Hochr.
36. *D. merika* Arènes
37. *D. pauciflora* Appleq.
38. *D. seyrigiana* Arènes
39. *D. tavia* Arènes
40. *D. tsiandrensis* Arènes
41. *D. tubulosoviscosa* Hochr.

APPENDIX 2. Formerly accepted species and infraspecific names synonymized in this treatment or changed in taxonomic status, with indication of the accepted names for each.

Dombeya ambongensis Arènes subsp. *sakarahae* Arènes [= *D. subviscosa* Hochr. subsp. *sakarahae* (Arènes) Appleq.]
Dombeya ambongensis Arènes var. *ambongensis* [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya ambongensis Arènes var. *fandrareensis* Arènes [= *D. subviscosa* Hochr. subsp. *sakarahae* (Arènes) Appleq.]
Dombeya ambongensis Arènes var. *ihosyensis* Arènes [= *D. subviscosa* Hochr. subsp. *ihosyensis* (Arènes) Appleq.]
Dombeya ambongensis Arènes f. *bevazahensis* Arènes [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya anakaensis Arènes subsp. *multiflora* Arènes [= *D. anakaensis* Arènes]
Dombeya analavelonae Arènes [= *D. ambalabeensis* Arènes subsp. *analavelonae* (Arènes) Appleq.]
Dombeya andilamenensis Arènes [= *D. aquifoliopsis* Hochr.]
Dombeya ankarafantsikae Arènes [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya australis Scott-Elliot subsp. *geayi* (Hochr.) Arènes [= *D. australis* Scott-Elliot subsp. *australis*]
Dombeya boeniensis Arènes [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya cloiselii Arènes [= *D. selinala* Arènes]
Dombeya coursii Arènes [= *D. merika* Arènes]
Dombeya decanthera Cav. subsp. *meridionalis* Arènes [= *D. decanthera* Cav. subsp. *decanthera*]
Dombeya decanthera Cav. var. *bojeriana* (Baill.) Arènes [= *D. decanthera* Cav. subsp. *decanthera*]
Dombeya farafanganica Arènes subsp. *farafanganica* [= *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.]
Dombeya farafanganica Arènes var. *linearis* Arènes [= *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.]
Dombeya farafanganica Arènes var. *manakensis* Arènes [= *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.]
Dombeya farafanganica Arènes [subsp. *endrina* Arènes] subvar. *endrina* [= *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.]
Dombeya farafanganica Arènes subvar. *latipetala* Arènes [= *D. decanthera* Cav. subsp. *latipetala* (Arènes) Appleq.]
Dombeya farafanganica Arènes subsp. *ramiovensis* Arènes [= *D. ramiovensis* (Arènes) Appleq.]
Dombeya lecomtei Hochr. subsp. *trichostyla* Arènes [= *D. lecomtei* Hochr.]
Dombeya lecomtei Hochr. var. *minoriflora* Hochr. [= *D. lecomtei* Hochr.]
Dombeya lecomtei Hochr. var. *valamainty* Arènes [= *D. lecomtei* Hochr.]
Dombeya mafimafy Arènes [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya majungensis Arènes [= *D. tubulosoviscosa* Hochr.]
Dombeya manaharica Baill. [= *D. decanthera* Cav. subsp. *farafanganica* (Arènes) Appleq.]
Dombeya mandoavato Arènes [= *D. lecomtei* Hochr.]
Dombeya meneriky Arènes [= *D. tulearensis* Arènes]
Dombeya subviscosa Hochr. var. *brevistaminodia* Arènes [= *D. subviscosa* Hochr. subsp. *subviscosa*]
Dombeya valafotsy Arènes [= *D. selinala* Arènes]
Dombeya vohitsiombeensis Arènes [= *D. selinala* Arènes]

APPENDIX 3. Index to Collectors. Collections are listed alphabetically by first collector's last name. Types are indicated in boldface. Numbers in parentheses correspond to those in the list of accepted species and subspecies.

Andriamihajarivo 1056 (16), *1098* (1), *1146* (13), *1683* (5c), *1736* (5c); *Andrianantoanina 151* (9); *Andrianjafy 1689* (20); *Applequist 248* (8b), *249* (5c × 8b), *255* (5c), *256* (8b), *257* (5c), *258* (8b), *262* (8b), *263* (5c), *264* (5c), *265* (8b), *266* (8b), *269* (28a), *270* (28a), *271* (28a), *272* (28a), *273* (28a), *274* (28a), *275* (28a), *276* (28a), *277* (28a).

Barnett 509 (28c); *Birkinshaw 425* (13), *449* (5a), *1318* (4), *1535* (26 × ?), *1648* (8a); *Boiteau 2533* (29), *2543* (33); *Bojer s.n.* (5a); *Bosser 9834* (4), *9836* (4), *17232* (18a), *17845* (33).

Capuron 1980 (**40**); *Chauvet 130* (20), *369* (18a × 20); *Cloisel 49* (26); *Commerson s.n.* (**5**); *Cours 271* (2), *275* (36), *1585* (36), *1663* (**36**), *5126* (29); *Croat 31072* (28c), *31073* (20), *31525* (24), *31945A* (33).

Debray s.n. Feb. 1972 (33); *Decary s.n.* 11 Mar. 1917 (24), *s.n.* 11 Mar. 1918 (24), *2542* (33), *2571* (33), *2632* (**21**), *2768* (33), *2993* (33), *3118* (**31**), *3505* (24), *3513* (24), *3544* (33), *3722* (**33**), *4169* (11), *4314* (13), *4660* (26), *4729* (5b), *4784* (**5b**), *5142* (**3**), *8478* (**24**), *8498* (24), *8554* (33), *8580* (33), *9049* (21), *9076* (33), *9542* (33), *9613* (33), *9931* (8a), *9934* (8a), *10177* (**13**), *13135* (**34**), *13173* (**32**), *16095* (**20**), *18530* (12), *18531* (**12**), *18924* (18a); *Déquaire 27507* (20), *27753* (**23**); *Descoings 628* (28), *649* (29), *2742* (26), *3239* (4), *3482* (28a); *Dorr 3057* (28a), *3991* (11); *Du Puy MB560* (29), *MB622* (20); *Dumetz 658* (11), *734* (11), *785* (11), *799* (14), *1164* (14).

Eboroke 797 (26), *812* (29), *996* (13 × 29).

Faliniaina 13 (11).

Gautier 4578 (**15**); *Geay 6717* (8a); *Gentry 11758* (22), *62096* (28A); *Gereau 3210* (14), *3359* (14); *Guillaumet 2485* (33).

Homolle 1434 (18a), *1752* (33); *Humbert 4090* (41), *12512* (**26**), *12688* (33), *12807* (29), *13047* (29), *13318* (**25**), *13331* (26), *13716* (33), *13758* (**10**), *13798* (**1**), *13813* (26), *14176* (33), *14177* (33), *14187* (38), *14316* (28c), *14333* (28c), *14453* (29); *19338* (18a), *19360* (18a), *19461* (**18**), *19757* (**18c**), *20192* (20), *28596* (28b), *28993* (14), *29019* (13), *29082* (5a), *29138* (26), *29152* (29), *29320* (**14**), *29552* (28c), *29562* (28c), *29650* (18a), *29659* (29); *Humblot 244* (5b).

Johnson s.n. (5a); *Jumelle 40* (**2**), *45* (**41**).

Keraudren 462 (28b), *815* (20), *1098* (18a), *1147* (36), *1539* (26), *1613* (19), *1619* (19), *1628* (19), *1675* (17).

Labat 2089 (20); *Leandri 4430* (26); *Lowry 5032* (33), *6730* (8a).

McPherson 14327 (11), *14767* (14), *14833* (11), *17148* (36); *Meyers 126* (28a); *Miller 10695* (**16**), *10704* (16); *Morat 3478* (18a), *4727* (18).

Nicoll 165 (20); *Noyes 1018* (28c).

Peltier 1357 (20), *5535* (18a), *5768* (18a), *Perrier de la Bâthie 594* (22), *1240* (41), *2186* (33), *2282* (28a), *5511* (**28**), *5516* (**35**), *5536* (**22**), *5617* (**2**), *12165* (**41**), *12166* (28a), *16656* (18a), *17732* (9), *17831* (35); *Petit s.n.* 1926 (**18b**), *s.n.* s.d. (35); *Phillipson 1726* (18a), *2488* (18a), *2499* (18a), *3104* (18a × 20), *3518* (33), *3532* (29), *5821* (33).

Rabarimanarivo 65 (5c); *Rabehevitra 941* (**30**); *Rabenantoandro 112* (5a), *351* (11), *421* (8b), *424* (8b), *793* (8b), *1768* (11); *Rabevohitra 1757* (11), *1798* (8a), *1894* (8a?), *2021* (11), *2051* (11 × 8a), *2101* (14), *2231* (29); *Rahantamalala 58* (20), *188* (28c); *Raharimampionona 75* (11); *Rajoharison 83* (8a), *181* (8b); *Rakotonandrasana 542* (5b); *Rakotonirina 277* (5c); *Rakotovao 5485* (33), *5493* (13); *Ramananjanahary 27* (19 × ?); *Ramison 214* (11), *241* (14), *370* (11); *Randriamampionona 117* (29), *133* (33), *288* (29), *420* (5a), *433* (5a), *835* (5a), *991* (13); *Randriambololona 87* (33); *Randrianaivo 97* (29), *862* (11), *1061* (18a), *1549* (29), *1718* (26); *Randrianasolo 342* (8a), *577* (11); *Randrianjanaka 169* (5b); *Randriatafika 73* (14), *365* (14), *711* (14); *Ranirison 591* (30); *Ratovoson 98* (13), *1265* (**17**), *1544* (26); *Ravololonanahary 93* (13); *Razafindraibe 179* (20); *Razafitsalama 579* (19), *1199* (16); *Razakamalala 1333* (30), *2470* (8b × 13?), *4271* (5a), *4329* (11), *4603* (8b); *Razanatsima 776* (**7**); *Reserves Naturelles 1867* (28a), *2123* (26), *2505bis* (29), *2509* (**29**), *2674* (26), *2749* (33), *2758* (26), *2760* (29), *2816* (28a), *2828* (28a), *2921* (28a), *3069* (**4**), *3145* (5b), *5022* (33), *5125* (28a), *5408* (28a), *5920* (5b), *6202* (26), *6207* (29), *6209* (26), *6753* (26), *6858* (35), *7351* (28a), *7742* (35), *8355* (26), *9180* (5b), *9440* (5a), *10070* (28a), *10289* (28a), *10305* (28a), *10692* (18a), *11445* (35) *13055* (5a); *Rogers 850* (29).

Scott Elliot 2524 (**8**); *Service Forestier 11* (28a), *17* [?] (28a), *28* (28a), *142* (28a), *369* (20), *511* (20), *2810* (**28c**), *3342* (28a), *3391* (18a), *3430* (33), *3489* (28a), *3531* (36), *3558* (19), *3556* (28a), *3802* (8b), *3960* (**39**), *4135* (18a), *4516* (20), *4535* (24), *4648* (18a), *4986* (18a), *5276* (**27**), *5292* (33), *5293* (29), *5357* (28a), *5744* (28a), *5876* (28a), *6765* (**40**), *7428* (8a), *8531* (26), *9209* (**8b**), *9223* (**11**), *10392* (28a), *11160* (18a), *11271* (**9**), *11638* (**28b**), *11716* (31), *11721* (33), *11783* (7a), *11821* (**6**), *11834* (26), *11836* (29), *11921* (28c × 20), *12391* (**5c**), *12943* (33), *13137* (**19**), *13736* (28b), *13789* (28b), *14012* (31), *14316* (24), *14480* (8b), *15081* (28a), *15598* (20), *15661* (21), *16200* (5c), *16370* (22), *16877* (36), *16938* (28a), *18110* (5b), *18536* (28a), *18598* (28c), *18697* (33), *19074* (28a), *19102* (28a), *19139* (28a), *19159* (28a), *19486* (28a), *19904* (28a), *20192* (20), *20441* (33), *20493* (33), *20504* (13), *20711* (18a), *20762* (20), *20988* (17), *22497* (29), *22499* (33), *22505* (33), *22510* (incertae sedis), *22533* (24), *22541* (24), *22590* (33), *22604* (29), *22612* (33), *22625* (29 × ?), *22628* (33), *22702* (30), *23242* (16), *23652* (5c), *23934* (8b), *26046* (28b × ?), *26053* (5a), *26789* (36), *28572* (6), *28576* (5a × ?), *29067* (18a), *29075* (**37**); *Seyrig 616* (**38**), *616B* (38); *Skema 52* (34); *Sussman 386* (18a).

Willing 35 (18a).

Zarucchi 7457 (8a).

NEW SUBFAMILY CLASSIFICATION FOR THE RUTACEAE

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ABSTRACT

Thirty-four species representing all subfamilies and tribes of the Rutaceae Juss. were included in phylogenetic analyses that utilize six molecular data sets from five chloroplast markers, three from the noncoding region (the *rps16* gene intron, the *trnL–trnF* intergenic spacer, and the *atpB–rbcL* spacer) and two from coding genic regions (*rbcL*, *atpB*), with the sixth marker from the *Xdh* nuclear gene. Based on the large number of nucleotide characters from the chloroplast and nuclear regions as well as the high levels of resolution and support from both parsimony and Bayesian analyses, the results are sufficiently robust to justify reclassification of the Rutaceae, with four subfamilies recognized in contrast to the traditional seven. This subfamily classification includes major rearrangements: (1) taxa within the subfamily Aurantioideae Horan. remain the same; (2) subfamily Cneoroideae Webb encompass the subfamilies Spathelioideae Engl. and Dictyolomatoideae Engl., *Harrisonia* R. Br. ex A. Juss. of the Simaroubaceae DC., *Cneorum* L. of the Cneoraceae Vest, and *Ptaeroxylon* Eckl. & Zeyh. of the Ptaeroxylaceae J.-F. Leroy; (3) subfamily Rutoideae Arn. include *Ruta* L. and *Chloroxylon* DC. of subfamily Flindersioideae Luerss.; and (4) subfamily Amyridoideae Link unite *Flindersia* R. Br. of subfamily Flindersioideae with subfamily Toddalioideae K. Koch and taxa previously included in subfamily Rutoideae.

Key words: Amyridoideae, Aurantioideae, Cneoroideae, Rutaceae, Rutoideae.

The Rutaceae Juss. are a large family of aromatic trees, shrubs, and herbs of approximately 2040 species in 150 to 170 genera (Kubitzki et al., 2011). The family has a more or less cosmopolitan distribution, but it is largely centered in the tropics and temperate regions of the Southern Hemisphere, especially Australia and South Africa. The bulk of the family occupies tropical and subtropical, montane or lowland habitats. Small components lie in the north- and south-temperate zones. The subfamilies Aurantioideae Horan. and Flindersioideae Luerss. are native to the Eastern Hemisphere, the subfamilies Spathelioideae Engl. and Dictyolomatoideae Engl. to the Western Hemisphere, and the subfamilies Toddalioideae K. Koch and Rutoideae Arn. to both hemispheres. Approximately one quarter of all species in the Rutaceae occur in the Western Hemisphere.

The Rutaceae is characterized by the following morphological features: the presence of secretory cavities containing aromatic ethereal oils usually scattered throughout the parenchyma and in the pericarp; sieve tubes with S-type plastids; exstipulate leaves; and a superior ovary (Chase et al., 1999). All other characters at this level manifest a bewildering diversity of character states, especially in floral and fruit morphology. Flowers are perfect or unisexual, actinomorphic or zygomorphic; sepals number from two to five and are distinct or connate at the base; petals usually number from two to five or are sometimes lacking and range from a few millimeters to several centimeters long; stamens number from two to 60 or more, and sometimes are reduced to staminodia; filaments are usually distinct but are rarely connate at the base or rarely adherent to adnate to the petals; and the placentation is axile when the ovary is plurilocular, marginal when the gynoecium is apocarpous or parietal when unilocular syncarous. Fruits range among capsules, samaras, schizocarps, drupes, berries, and hesperidia, with endosperm present or lacking. Due to this level of diversity in the above characters, they are not useful at the subfamily level (Chase et al., 1999).

In addition to diverse morphological features, the biochemical networks and pathways of the Rutaceae produce a tremendous spectrum of secondary metabolites and a wide range of resistances to biotic and abiotic stresses. For instance, Price (1963) stated that the Rutaceae are the most chemically versatile of all plant families. These chemical compounds, including limonoids, flavonoids, coumarins, and alkaloids possess antimicrobial activity (Esterhuizen et al., 2006), herbicidal activity (Aliotta et al., 1996), trypanocidal activity (Ambrozin et al., 2004), insecticidal activity (Marr & Tang, 1992; Rajkumar & Jebanesan, 2008), and antimalarial activity (Fernandez et al., 2009).

In the only systematic treatment of the Rutaceae, Engler (1896, 1931) recognized seven subfamilies: Rhabdodendroideae Engl., Aurantioideae, Spathe-

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lioideae, Dictyolomatoideae, Flindersioideae, Rutoideae, and Toddalioideae. He circumscribed these subfamilies primarily by characters of the gynoecium, especially fruit type. Analysis of *rbcL* sequence data by Gadek et al. (1996) placed *Rhabdodendron* Gilg & Pilg. as sister to the caryophyllid clade, a result also found by Fay et al. (1997) and, more recently, Brockington et al. (2009) and supported by biochemical studies of Wolter-Filho et al. (1985). Based on these conclusive results, *Rhabdodendron* is excluded from this study, as is consideration of its subfamily Rhabdodendroideae. Below is a summary of the remaining six subfamilies for the Rutaceae as included in the current analyses, as had been defined by Engler (1896, 1931).

1. Rutaceae subfam. Aurantioideae Horan. In recent gene analyses (Samuel et al., 2001; Araujo et al., 2003; Morton et al., 2003; Bayer et al., 2009; Morton, 2009) all genera of subfamily Aurantioideae comprise a very strongly supported monophyletic group that is defined by a number of morphological, cytological, and chemical synapomorphies (Waterman, 1975; Grieve & Scora, 1980; Samuel et al., 2001; Morton et al., 2003).

2–3. Subfamilies Spathelioideae Engl. and Dictyolomatoideae Engl. subfam. Dictyolomatoideae consist of the South American genus *Dictyoloma* A. Juss. The subfamily Spathelioideae also consist of a single genus, *Spathelia* L., native to the West Indies and South America. Morton et al. (1996), Chase et al. (1999), Gruppo et al. (2008 [excluding *Harrisonia* R. Br. ex A. Juss.]), Razafimandimbison et al. (2010), and Appelhans et al. (2011), found the consistent pairing with strong support of *Dictyoloma* and *Spathelia* within a moderately supported clade that included *Cneorum* L., *Ptaeroxylon* Eckl. & Zeyh., and *Harrisonia*.

4. Subfamily Flindersioideae Luerss. Engler (1896, 1931) assigned two genera to subfamily Flindersioideae, *Flindersia* R. Br. and *Chloroxylon* DC., both native to the Old World tropics. Morton et al. (1996) and Chase et al. (1999), using molecular data, confirmed that these two genera are not members of the Meliaceae Juss., but rather belong to the Rutaceae. The above two authors and Gruppo et al. (2008) recovered a supported relationship for *Flindersia* forming a clade with *Lunasia* Blanco (subfamily Rutoideae) while *Chloroxylon* formed a clade with *Ruta* L. (subfamily Rutoideae), suggesting the non-monophyly of the subfamily.

5–6. Subfamilies Rutoideae Arn. and Toddalioideae K. Koch. The subfamily Rutoideae are the largest of the subfamilies with approximately 100 genera and 1204 species from temperate and tropical regions worldwide. Five tribes are currently recognized (sensu Engler, 1896, 1931): the Boroniinae Bartl. (19 genera), Galipeeae Kallunki (28 genera), Diosmeae DC. (13 genera), Ruteae Juss. (seven genera), and Zanthoxyleae Dumort. (32 genera). Engler (1896, 1931) defined the subfamily Toddalioideae (Dendrologie 1: 564. 1869) as consisting of approximately 21 genera and 152 species, also native to tropical and temperate regions worldwide, as a separate subfamily. However, revisionary studies by Hartley (1974, 1977, 1981, 1982) indicated that those genera of subfamily Toddalioideae with syncarpous, drupaceous fruits (e.g., *Acronychia* J. R. Forst. & G. Forst., *Toddalia* Juss., and *Phellodendron* Rupr.) were more closely related to genera of subfamily Rutoideae with apocarpous or subapocarpous follicular fruits (e.g., *Melicope* J. R. Forst. & G. Forst., *Zanthoxylum* L., and *Tetradium* Lour.). Morton et al. (1996) and Chase et al. (1999) revealed that the subfamily is paraphyletic, with taxa from subfamilies Toddalioideae and Flindersioideae nested within subfamily Rutoideae. Poon et al. (2007) examined 12 genera of the subfamilies Rutoideae and Toddalioideae and found once again that these were not monophyletic groups. This study also showed that the genus *Euodia* J. R. Forst. & G. Forst. was polyphyletic while the monophyly of *Zanthoxylum* was ambiguous. *Tetradium* was closely related to *Phellodendron*, *Toddalia*, and *Zanthoxylum*, and was called the proto-Rutaceae group. Poon et al. (2007) used a limited number of genera and genes in their study, thus much more data are needed before a reliable phylogeny can be established. Elucidation of the phylogeny of Rutaceae and subfamily Rutoideae is important as its members possess unique metabolic pathways with capabilities for the production of diverse and complex Rutalean metabolites that have demonstrated a wide range of known chemical activities with the potential for other valuable activities.

In summary, Morton et al. (1996, 2003), Chase et al. (1999), Bayer et al. (2009), and Morton (2009) concluded the following: (1) that the Simaroubaceae DC. and Meliaceae are the closest relatives of Rutaceae; (2) that subfamily Aurantioideae are monophyletic; (3) that subfamily Flindersioideae belong in the Rutaceae but are not monophyletic, and that the two genera (*Flindersia* and *Chloroxylon*) appear to be related to different genera in the subfamily Rutoideae; (4) that the subfamilies Dictyolomatoideae and Spathelioideae, each monogeneric, are by default monophyletic, but both are part of a clade that includes *Harrisonia*, *Cneorum*, and *Ptaeroxylon*; (5) that subfamily Toddalioideae should

be merged with subfamily Rutoideae; and (6) that the Rutaceae, are paraphyletic, and monophyly can be achieved perhaps by the inclusion of *Harrisonia*, *Cneorum*, and *Ptaeroxylon* in a recircumscribed subfamily Spathelioideae. Gruppo et al. (2008) came to the exact same conclusions but added that none of the tribes with more than one genus is monophyletic (except Diosmeae) and that traditionally used characters at the subfamily and tribal level are not useful.

Recent molecular phylogenetic gene studies of the remaining six subfamilies for the Rutaceae include Chase et al. (1999), Scott et al. (2000), Poon et al. (2007), Gruppo et al. (2008), Morton et al. (2003), Bayer et al. (2009), Morton (2009), Razafimandimbison et al. (2010), and Appelhans et al. (2011). These studies have analyzed, at most, 59 genera out of a total of 160 genera of Rutaceae, using 10 chloroplast genes and one nuclear gene. In order to redefine the family and subfamilies, a more complete survey of the Rutaceae genera with a consistent increased use of molecular markers is required.

The current study utilized six genomic regions, including five chloroplast markers and one nuclear gene. This reflects the most comprehensive coverage using molecular data at the family level. Three of the chloroplast genome regions analyzed were from the noncoding region: the *rps16* gene intron, the *trnL–trnF* intergenic spacer, and the *atpB–rbcL* spacer. The intron of the *rps16* is a group II intron that was first used for phylogenetic studies by Oxelman et al. (1997). The *trnL–trnF* region consists of the *trnL* intron and the *trnL–trnF* intergenic spacer (Taberlet et al., 1991). The *atpB–rbcL* spacer lies between the gene for the large subunit of ribulose-1-5-bisphosphate-carboxylase (*rbcL*) and the gene for the beta subunit of the chloroplast ATP-synthase (*atpB*).

Both the *rbcL* and *atpB* genes are located in the large single-copy region of the plastid genome; their coding sequences are on opposite strands separated by an intergenic spacer of approximately 600–800 bp. The genes code for distinct enzymatic functions: *rbcL* codes for the large subunit of the ribulose-1-5 bisphosphate-carboxylase/oxygenase, a soluble enzyme in the stroma that functions in both the light-dependent and light-independent (Calvin cycle) reactions, whereas *atpB* codes for the beta subunit of the ATP synthase complex, which is bound to the thylakoid membrane and is the site of the light-dependent reactions of photosynthesis. The *atpB* gene is contiguous with the *atpE* gene and downstream from the *rbcL* gene (Zurawski et al., 1982).

Xanthine dehydrogenase (*Xdh*), the nuclear gene, is a member of the molybdenum (Mo) hydroxylase family of enzymes that play important metabolic roles in purine metabolism and plant hormone biosynthesis (Mendel & Hansch, 2002). Among Mo-enzymes, the alignment of amino acid sequences permits domains that are well conserved to be defined although highly variable. This gene is located on chromosome 4, contig fragment 82 (Morton, pers. obs.). The *Xdh* gene is approximately 4262 bp long, and the sequenced segment lies from 363 to 1719 bps. This segment contains approximately four indel regions. To date, only one copy has been reported, except in silkworms and *Arabidopsis* Heynh., in which a second copy has been examined (Hesberg et al., 2004).

Materials and Methods

Selection of Taxa

Thirty-four species representing all subfamilies and tribes of Rutaceae were included in the analysis. Similar exemplar species of Rutaceae, which were used in the *rbcL* and *atpB* analysis of Chase et al. (1999), have been used in this study. Representatives of families that have been suggested as relatives of Rutaceae (Fernando & Quinn, 1995; Chase et al., 1999) have also been included, e.g., the Cneoraceae, Meliaceae, Ptaeroxylaceae, and Simaroubaceae s. str.

DNA Extraction, Amplification, and Sequencing

Total genomic DNA was isolated from fresh or desiccant-dried leaf tissue or from herbarium material. DNA preparation either followed the same procedures as Chase et al. (1999), or by extraction with the Plant DNeasy Mini Kit (Qiagen, Clifton Hill, Victoria, Australia). The 50-µl (chloroplast DNA; cpDNA) and 25-µl (nuclear ribosomal DNA; nrDNA) volume reactions were constituted in a buffer of 20 mM Tris HCl (pH 8.4) buffer, and 50 mM KCl and utilized, 3 mM $MgCl_2$, 200 uM dNTPs, 1 uM of each primer, and 1.25 U (cpDNA) and 0.75 U (nrDNA) of Taq polymerase (Invitrogen, Carlsbad, California, U.S.A.). With the reactions on ice, 100–500 ng of template total DNA was added, and then tubes were placed in the thermal cycler (Biometra, Goettingen, Germany). Primers and cycle reactions for the six markers are reported in Table 1.

The PCR products were cleaned using the QIAquick PCR purification kit (QIAGEN Inc., Chatsworth, California, U.S.A.), following the manufacturer's protocols and eluting with double distillated water (Millipore, Billerica, Massachusetts, U.S.A.). Clean products were directly sequenced, using the ABI PRISM Dye Terminator Cycle Sequencing Ready Kit with AmpliTaq DNA Polymerase (Applied Biosystems Inc., Foster City,

Table 1. Primers and PCR protocols.

DNA region	Primer name	Reference	Initial denaturing	Cycles	Denaturing	Primer annealing	Extension	Final extension
rbcL	1F 1460R 636F 724R	Olmstead et al., 1992	—	35	1 min. at 95°C	30 sec. at 50°C	1 min. at 72°C	
atpB	2F 1492R 611F 766R	Hoot et al., 1995	—	35	1 min. at 95°C	30 sec. at 50°C	1 min. at 72°C	
atpB–rbcL spacer	520F 3158R	Crayn & Quinn, 2000	—	35	1 min. at 95°C	30 sec. at 50°C	1 min. at 72°C	7 min. at 72°C
rps16	rpsF rpsR2	Oxelman et al., 1997	—	25	30 sec. at 95°C	50 sec. at 57°C	2 min. at 72°C	
trnL–trnF	trn-c trn-d trn-e trn-f	Taberlet et al., 1991	7 min. at 94°C	30	1 min. at 94°C	1 min. at 45°C	1 min. at 72°C	7 min. at 72°C
Xdh	486F 1365R 1296F 1869R	Morton, 2011	1 min. at 96°C	34	30–60 sec. at 94°C	1 min. at 48°C–60°C	1 min. at 68°C–72°C	7 min. at 72°C

Table 2. GenBank accession numbers for molecular data sets from five chloroplast markers, three from the noncoding region (the *rps16* gene intron, the *trnL–trnF* intergenic spacer, and the *atpB–rbcL* spacer) and two from coding genic regions (*rbcL*, *atpB*), as well as a sixth marker from the *Xdh* nuclear gene. Newly sequenced taxa for this study are in bold with voucher information. All remaining GenBank accession numbers are from previous studies, as indicated by footnotes. Collection abbreviations are M. W. Chase (MWC) and C. M. Morton (CMM). NA, not applicable. References indicated by subscript after number and papers listed below.

	Voucher	*rbcL*	*atpB*	*atpB–rbcL* spacer	*trnL*	*rps16*	*Xdh*
Adenandra uniflora (L.) Willd.	South Africa. *MWC 1769*, K	AF066803[a]	AF066832[a]	AM502754 (*A. villosa* Eckl. & Zeyh.)[p]	JX307298	JX307327	JX307301
Aegle marmelos (L.) Corrêa	Indonesia. *MWC 1340*, K	AF066811[a]	AF066839[a]	FJ434197[g]	AY295294[h]	AY295268[h]	JX307302
Atalantia ceylanica Oliv.	Indonesia. *MWC 1341*, K	AF066812[a]	AF066840[a]	FJ434186[g]	AY295288[h]	AY295262[h]	JX307303
Calodendrum capense Thunb.	South Africa. *MWC 1821*, K	AF066805[a]	AF066834[a]	JX307335	AF025511[k]	JX307328	JX307304
Casimiroa edulis La Llave & Lex.	NA	AF066808[a]	AF066837[a]	EF126506[f]	EU853782 (*C. tetrameria* Millsp.)[j]	EF126573[f]	EU264403[q]
Chloroxylon swietenia DC.	Indonesia. *MWC 1291*, K	AF066802[a]	AF066831[a]	FJ434177[g]	AY295276[h]	AY295250[h]	JX307305
Choisya mollis Standl.	United States. *MWC 1755*, K	AF066800[a]	AF066829[a]	EF126507 (*C. ternate* Kunth)[f]	EU853784[j]	EU853730[j]	JX307306
Chorilaena quercifolia Endl.	Australia. *M. Richardson s.n.*, CBG	AF066810[a]	AF066838[a]	JX307336	EU853785[j]	EU853731[j]	JX307307
Clausena excavata Burm. f.	Indonesia. *MWC 1343*, K	AF066813[a]	AF066841[a]	FJ434179[g]	EF126674[f]	AY295258[h]	JX307308
Cneorum pulverulentum Vent.	Spain. *MWC 3428*, K	U38858[c]	AF066828[a]	JX307337	EU853787[j]	EU853733[j]	JX307309
Correa pulchella J. Mackay ex Sweet	Australia. *MWC 1757*, K	AF066816[a]	AF066844[a]	JX307338	EU853790[j]	EU853736[j]	JX307310
Dictamnus albus L.	Australia. *MWC 1820*, K	AF066801[a]	AF066830[a]	JX307339	EU853792[j]	EU853738[j]	JX307311
Dictyoloma vandellianum A. Juss.	Brazil. *Pirani et al. 3039*, K	AF066823[a]	AF066853[a]	JX307340	EU853793[j]	EU853739[j]	JX307312
Diplolaena dampieri Desf.	Australia. *M. Richardson s.n.*, CBG	AF066807[a]	AF066836[a]	JX307341	EU853794[j]	EU853740[j]	JX307313
Eremocitrus glauca (Lindl.) Swingle	NA	AF066819[a]	AF066847[a]	FJ434188[g]	AY295293[h]	AY295267[h]	EU264414[q]
Eriostemon angustifolius Paul G. Wilson	Australia. *MWC 2005*, K	AF156883 (*E. brevifolius* A. Cunn. ex Endl)[a]	AF156882 (*E. brevifolius* A. Cunn. ex Endl)[a]	JX307342	JX307299	JX307329	JX307314
Flindersia australis R. Br.	Australia. *I. R. Telford 11032*, CBG	U38861[c]	EF118872[f]	JX307343	EF126677[f]	EF126610[f]	JX307315
Fortunella polyandra (Ridl.) Tanaka	NA	AF066799 (*Fortunella japonica* Swingle)[a]	AF066827 (*Fortunella* sp. Swingle)[a]	FJ434187[g]	AY295291[h]	AF320273 (*F. hindsii* Swingle)[h]	EU264397[q]

Table 2. Continued.

	Voucher	*rbcL*	*atpB*	*atpB–rbcL* spacer	*trnL*	*rps16*	*Xdh*
Glycosmis pentaphylla (Retz.) DC.	Indonesia. *MWC 1345*, K	AF066820[a]	AF066849[a]	FJ434178[g]	AY295279[h]	AY295253[h]	JX307316
Harrisonia perforata (Blanco) Merr.	Indonesia. *CMM 1996-10*, CM	U38863[c]	JX307295	JX307344	EU721390 (*H. abyssinica* Oliv.)[r]	—	JX307317
Lunasia amara Blanco	Indonesia. *MWC 1347*, K	AF066814[a]	AF066842[a]	JX307345	EU853805[j]	EU853753[j]	—
Melicope ternata J. R. Forst. & G. Forst.	Australia. *MWC 1759*, K	AF116271[a]	AF066826[a]	JX307346	EU852808[j]	EU853756[j]	EU264401[q]
Murraya paniculata (L.) Jack	cult. United States. *CMM 2012-1*, CM	EF119891[a]	JX307296	FJ434180[g]	EU853810[j]	AF320268°	—
Phebalium woombye (Bailey) Domin	Australia. *H. Fernanado 1402*, CBG	AF066822[a]	AF066852[a]	JX307347	JX307300	—	JX307318
Phellodendron amurense Rupr.	cult. Australia. *MWC 1771*, K	AF066804[a]	AF066833[a]	JX307348	DQ225993[l]	JX307330	JX307319
Pilocarpus pennatifolius Lem.	cult. Australia. *MWC 1760*, K	AF066809[a]	AF066825[a]	JX307349	EU853811 (*P. spicatus* A. St.-Hil.)[j]	EU853761 (*P. spicatus* A. St.-Hil.)[j]	EU264408[q]
Poncirus trifoliata (L.) Raf.	NA	AJ235806[b]	AJ238409[a]	FJ434181[g]	AY295282[h]	AY295256[h]	EU264398[q]
Ptaeroxylon obliquum Radlk.	cult. South Africa. *Baker s.n.*, BOL	AF123276[d]	AF066848[a]	JX307350	EU853812[j]	EU853762[j]	JX307320
Ruta graveolens L.	NA	RGU39281[d]	AF035913[a]	FJ434173[g]	AY295275[h]	AY295249[h]	EU264412[q]
Ravenia infelix Vell.	Brazil. *J. Kallunki et al. 614*, NY	JX307294	JX307297	JX307351	EU853814[j]	EU853764[j]	EU264411[q]
Sarcomelicope simplicifolia (Endl.) T. G. Hartley	Australia. *MWC 1762*, K	AF066817[a]	AF066845[a]	JX307352	EU853816[j]	EU853766[j]	JX307321
Severinia buxifolia (Poir.) Ten.	cult. United States. *CMM 2012-2*, CM	AF066806[a]	AF066835[a]	FJ434183[g]	EU369566[i]	AY295264[h]	JX307322
Skimmia anquetilia N. P. Taylor & Airy Shaw	cult. Australia. *MWC 1766*, K	AF066818[a]	AF066846[a]	EF126564[f]	EU853819 (*S. japonica* Thunb.)[j]	EF126630[f]	JX307323
Spathelia excelsa (K. Krause) R. S. Cowan & Brizicky	NA	AF066798[a]	AF066854[a]	—	EU853820[j]	EU853770[j]	EU264413[q]
Zanthoxylum monophyllum (Lam.) P. Wilson	NA	U39282[a]	AF035919[a]	EF362484[f]	EU853773 (*Z. rhoifolium* Lam.)[j]	EF126633[f]	EU264402[q]
Zanthoxylum fagara (L.) Sarg.	Mexico. *Henrickson 22590*, CM	AF066815[d]	AF066843[a]	EF126549[f]	EF126684[f]	JX307331	JX307324

Table 2. Continued.

	Voucher	*rbcL*	*atpB*	*atpB–rbcL* spacer	*trnL*	*rps16*	*Xdh*
Outgroup Taxa							
Ailanthus altissima (Mill.) Swingle	United States. *H. George s.n.*, CM	L12566[c]	AF035895[a]	JX307353	FN599505	JX307332	EU264405[q]
Trichilia emetica Vahl	Unknown. *MWC 552*, K	U39082[d]	AF066851[a]	JX307354	FJ039160 (*T. surinamensis* C. DC.)[a]	JX307333	JX307325
Simaba bidwillii (Hook. f.) Feuillet	Australia. *Fernando et al. 1995*, QRS	U38926[c]	AF066824 (*S. baileyana* (Oliv.) Feuillet)[a]	JX307355	EU853818 (*S. cedron* Planch.)[j]	EU853768 (*S. cedron* Planch.)[j]	JX307326
Swietenia macrophylla King	cult. United States. *MWC 250*, NCU	U39080[d]	AF066857[a]	JX307356	EF489262[m]	JX307300	EU264415[q]

[a] Chase et al., 1999.
[b] Chase et al., 1993.
[c] Fernando & Quinn, 1995.
[d] Gadek et al., 1996.
[e] Gadek et al., 1992.
[f] Bayer et al., 2009.
[g] Morton, 2009.
[h] Morton et al., 2003.
[i] Li et al., 2007.
[j] Gruppo et al., 2008.
[k] Scott et al., 2000.
[l] Poon et al., 2007.
[m] Salvo et al., 2008.
[n] Buerki et al., 2009.
[o] Samuel et al., 2001.
[p] Trinder-Smith et al., 2007.
[q] Morton, 2011.
[r] Buerki et al., 2009.

California, U.S.A.). Unincorporated dye terminators were removed using the DyeEx dye-terminator removal system (QIAGEN Inc.), following the manufacturer's recommendations. Samples were then loaded into an ABI 3100 DNA Sequencer (ABI, Grand Island, New York, U.S.A.). The sequencing data were analyzed and edited using the Sequencher software program (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A.).

PHYLOGENETIC ANALYSIS

Boundaries of the above gene regions were determined by comparison with sequences in GenBank. The following alignment criteria and methodology were used: (1) when two or more gaps were not identical but overlapping, they were scored as two separate events; and (2) phylogenetically informative indels (variable in two or more taxa) were scored as one event at the end of the dataset. All DNA sequences reported in the analyses have been deposited in GenBank (Table 2).

For phylogenetic analysis, the data sets were examined using maximum parsimony and Bayesian analyses. Maximum parsimony analyses used the heuristic search option in PAUP* 4.0b8 (Swofford, 2002), with uninformative characters excluded. Searches were conducted with 1000 random-taxon-addition replicates with TBR branch swapping, steepest descent and MulTrees selected, and with all characters and states weighted equally and unordered. All trees from the replicates were then swapped onto completion, all shortest trees were saved, and a consensus tree was computed. Relative support for individual clades was estimated with the bootstrap method (Felsenstein, 1985). One thousand pseudoreplicates were performed with uninformative characters excluded. Ten random-taxon-addition heuristic searches for each pseudoreplicate were performed, and all minimum-length trees were saved for each search. To reduce bootstrap search times, branches were collapsed if their minimum length was zero ("amb-").

Bayesian analyses were performed using MrBayes 3.1.1 (Ronquist et al., 2005) on the combined molecular datasets. The substitution model for each DNA region was selected with MrModeltest 2.3 (Nylander, 2004) under the Akaike information criterion (AIC). The parameters for the Bayesian analyses were as follows: nst = 6; rates = Invgamma; set autoclose = yes; mcmcp ngnen = 1000000; prinfewq = 100; samplefreq = 10; savebriens = yes. The first 25% of the trees were regarded as "burn in" and omitted, and the majority rule consensus tree was obtained in PAUP* from the remaining trees.

To determine the combinability of the two datasets, their data structures were compared using methods outlined by Mason-Gamer and Kellogg (1996), who discussed various ways to assess conflict between datasets. In one method the combination of independent datasets is possible if the trees do not conflict or if conflict receives low bootstrap support. Therefore, each node on the independent trees is tested for congruence against the other. If the nodes do not contain conflicting information, they are congruent and the datasets are combinable. Where there are incongruent nodes, the bootstrap values for each node are examined. If the support is less than 75%, then there is no hard conflict and the incongruence is interpreted as being due to chance. In this study the different datasets were also analyzed in combination to see how each dataset confirmed or differed from the tree topologies from the other datasets and to adopt a hypothesis of phylogenetic relationships for the subfamilies.

Results

The inclusion of gap coding in all datasets containing molecular data resulted in more homoplasy and lack of resolution; therefore, gap coding was not used in the following results. GenBank sequences JX307295–JX307356 were generated specifically for this study (Table 2).

rbcL

No gaps were required for proper alignment of the 40 *rbcL* sequences. Mean percentage G + C content is 45%. Of the 1410 positions constituting the aligned *rbcL* sequences, 307 (22%) were variable and 157 (11%) were parsimony-informative. The analysis recovered 18,352 equally optimal trees of 406 steps (CI = 0.50, RI = 0.68; cf. Fig. 1).

The Rutaceae s.l. were supported as monophyletic in the strict consensus tree. Basal within the majority rule tree, the Rutaceae s.l. consisted of two main clades, the weakly supported clade comprised by the (*Cneorum pulverulentum* Vent, Cneoraceae + *Ptaeroxylon obliquum* Radlk., Ptaeroxylaceae; BS 89%) clade sister to the ((*Dictyoloma vandellianum* A. Juss. + *Spathelia excelsa* (K. Krause) R. S. Cowan & Brizicky; BS 97%) + *Harrisonia perforata* (Blanco) Merr., Simaroubaceae) clade, and a moderately supported major clade comprising the rest of the family (BS 89%). Within the largest clade, three pairs of genera were supported with bootstrap values greater than 75%; these are, starting from the base: (1) the strongly supported (BS 100%) pair composed by *Severinia buxifolia* (Poir.) Ten. and *Atalantia*

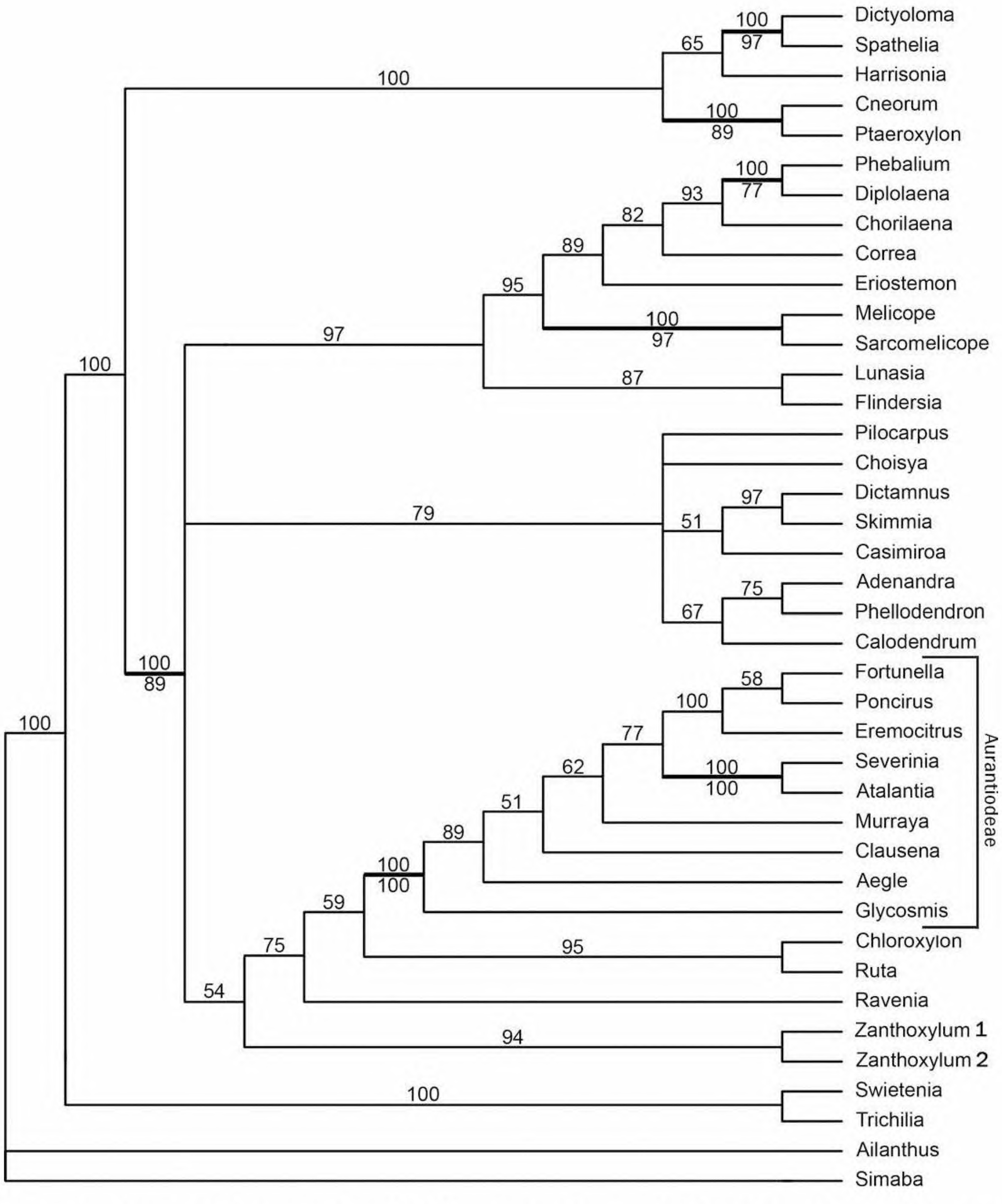


Figure 1. The majority rule consensus tree of 18,352 most-parsimonious trees (length = 406 steps, CI = 0.50, RI = 0.68) obtained from the *rbcL* data from the Rutaceae. The bracket indicates the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

ceylanica Oliv., which was included in the well-supported Aurantioideae clade (BS 100%; Fig. 1); (2) the clade comprising *Melicope ternata* J. R. Forst. & G. Forst. and *Sarcomelicope simplicifolia* (Endl.) T. G. Hartley (BS 97%); and (3) the clade consisting of *Phebalium woombye* (Bailey) Domin and *Diplolaena dampieri* Desf. (BS 77%).

ATPB

No gaps were required for proper alignment of the 40 *atpB* sequences. Mean percentage G + C content is 44%. Of the 1489 positions constituting the aligned *atpB* sequences, 292 (20%) were variable and 153 (10%) were parsimony-informative. The

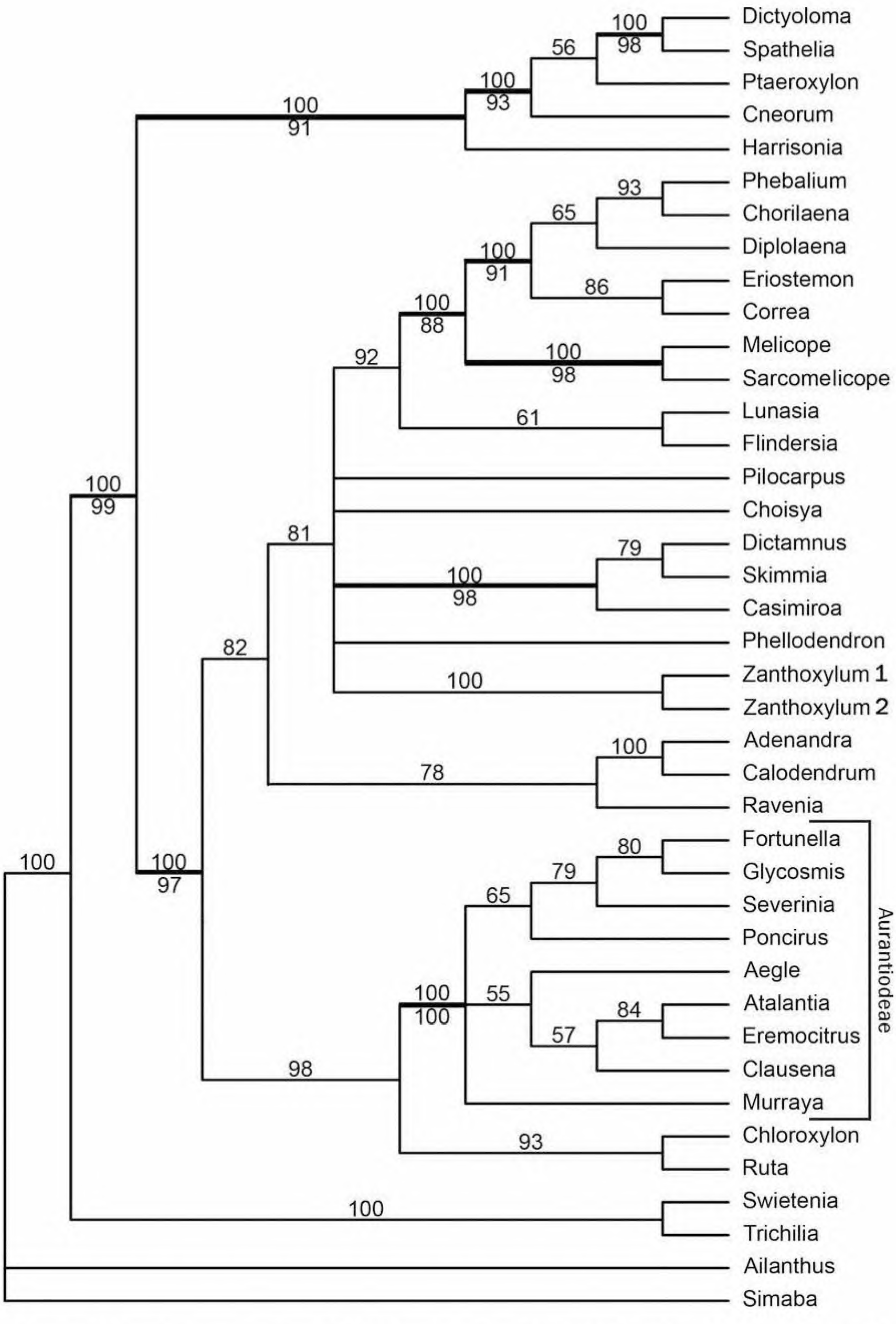


Figure 2. The majority rule consensus tree of 9763 most-parsimonious trees (length = 353 steps, CI = 0.53, RI = 0.72) obtained from the *atpB* data from the Rutaceae. The brackets indicate the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

analysis recovered 9763 equally optimal trees of 353 steps (CI = 0.53, RI = 0.72; cf. Fig. 2).

The Rutaceae s.l. were supported as monophyletic in the strict consensus tree (BS 99%). Basal within the majority rule tree, the Rutaceae s.l. clade was a clade (BS 91%) comprised of *Harrisonia perforata*, Simaroubaceae sister to the clade ((*Dictyoloma vandellianum* + *Spathelia excelsa*; BS 98%) + *Ptaeroxylon obliquum*, Ptaeroxylaceae + *Cneorum pulverulentum*, Cneoraceae; BS 93%). The rest of the family exemplars (BS 97%) consisted of small clades. Clades that contained bootstrap support greater than 75%, starting from the base, include: (1) a clade containing members of the subfamily Aurantioideae

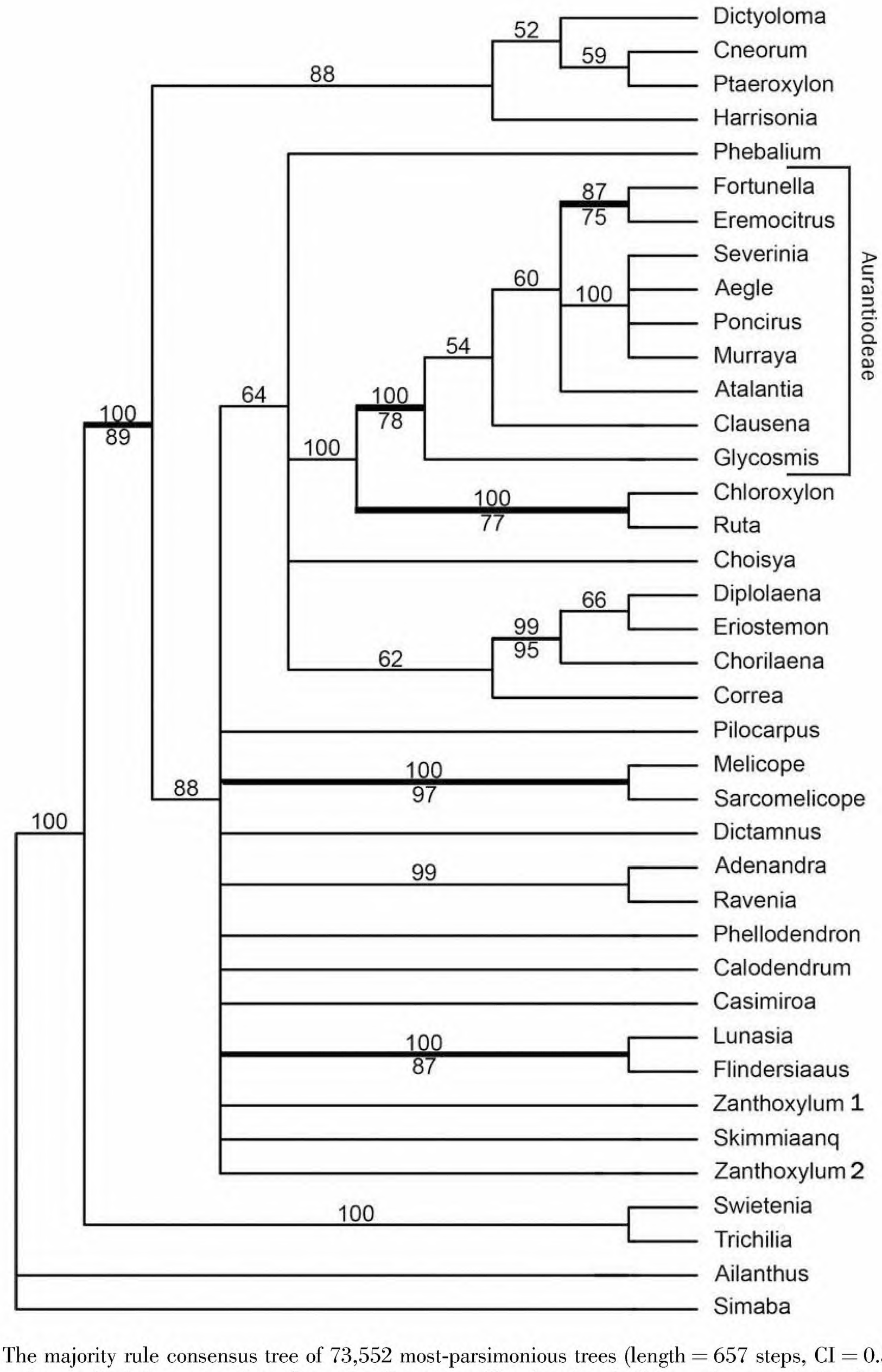


Figure 3. The majority rule consensus tree of 73,552 most-parsimonious trees (length = 657 steps, CI = 0.53, RI = 0.65) obtained from the *atpB–rbcL* spacer data from the Rutaceae. The bracket indicates the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

(BS 100%); (2) a clade containing (*Casimiroa edulis* La Llave & Lex, *Dictamnus albus* L., and *Skimmia anquetilia* N. P. Taylor & Airy Shaw; BS 98%); and (3) a clade (BS 88%) containing ((*Melicope ternata* + *Sarcomelicope simplicifolia*; BS 98%) sister to a clade containing (*Phebalium woombye*, *Chorilaena quercifolia* Endl., *Diplolaena dampieri*, *Eriostemon angustifolius* Paul G. Wilson, and *Correa pulchella* J. Mackay ex Sweet; BS 91%)).

RBCL–ATPB SPACER

Approximately 16 gaps were required for proper alignment of the 39 sequences (*Spathelia* not

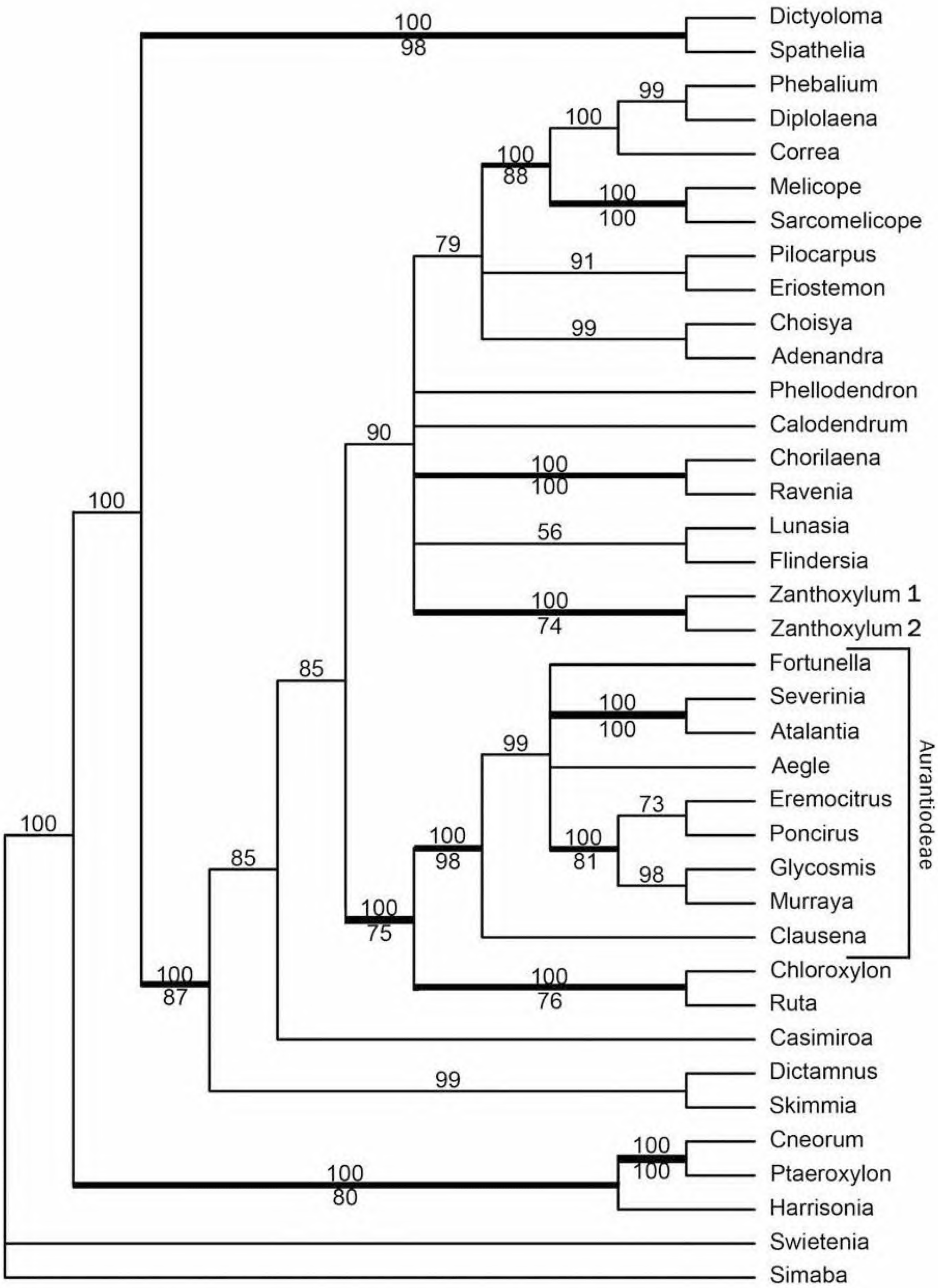


Figure 4. The majority rule consensus tree of 12,791 most-parsimonious trees (length = 1608 steps, CI = 0.63, RI = 0.53) obtained from the *trnL–trnF* data from the Rutaceae. The bracket indicates the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

sequenced) for *rbcL–atpB* spacer. These gaps ranged from one to 29 bps. None of these gaps were parsimony-informative. Mean percentage G + C content is 34%. Of the 987 positions constituting the aligned sequences, 452 (46%) were variable and 222 (23%) were parsimony-informative. The analysis recovered 73,552 equally optimal trees of 657 steps (CI = 0.53, RI = 0.65; cf. Fig. 3).

The Rutaceae s.l. was supported as a monophyletic clade in the strict consensus tree (BS 89%). Most of the Rutaceae consisted of a polytomy in the majority rule tree except for several small clades with bootstrap support greater than 75%, which included: (1) the (*Lunasia amara* Blanco + *Flindersia australis* R. Br.; BS 87%) clade; (2) the (*Melicope ternata* + *Sarcomelicope simplicifolia*; BS 97%) clade; (3) the

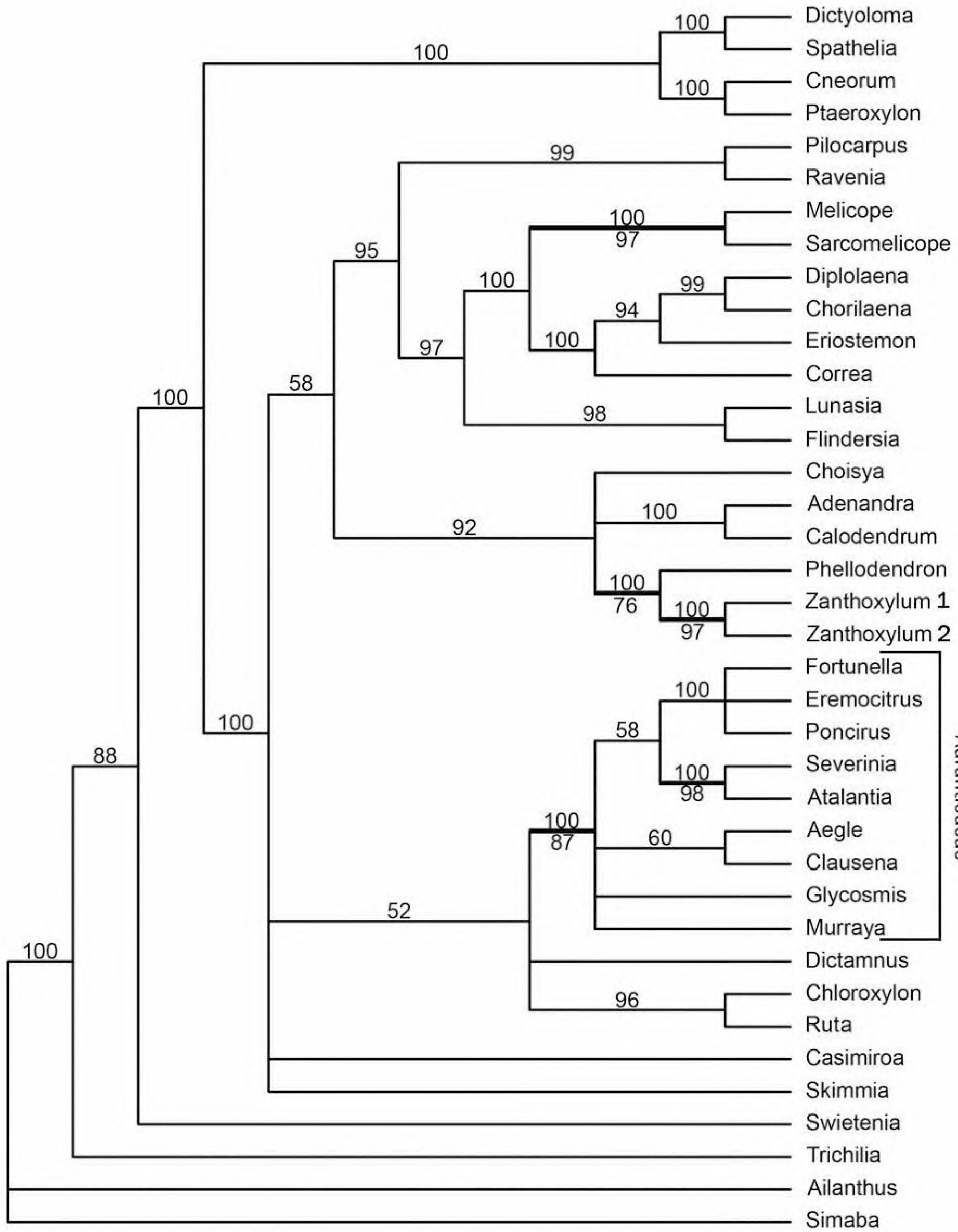


Figure 5. The majority rule consensus tree of 2172 most-parsimonious trees (length = 1643 steps, CI = 0.59, RI = 0.52) obtained from the *rps16* data from the Rutaceae. The bracket indicates the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

clade (*Diplolaena dampieri*, *Eriostemon angustifolius* + *Chorilaena quercifolia*; BS 95%); (4) the clade containing members of the subfamily Aurantioideae (BS 78%) with the (*Fortunella polyandra* (Ridl.) Tanaka + *Eremocitrus glauca* (Lindl.) Swingle; BS 75%) clade internally supported; and (5) the clade (*Chloroxylon swietenia* DC. + *Ruta graveolens* L.; BS 77%).

TRNL–TRNF

Approximately 29 gaps were required for proper alignment of the 39 sequences (*Ailanthus* Desf. not sequenced) for *trnL–trnF*. These gaps ranged from one to 41 bps. None of these gaps were parsimony-informative. Mean percentage G + C content is 36%. Of the 1039 positions constituting the aligned sequences, 612 (60%) were variable and 427 (40%)

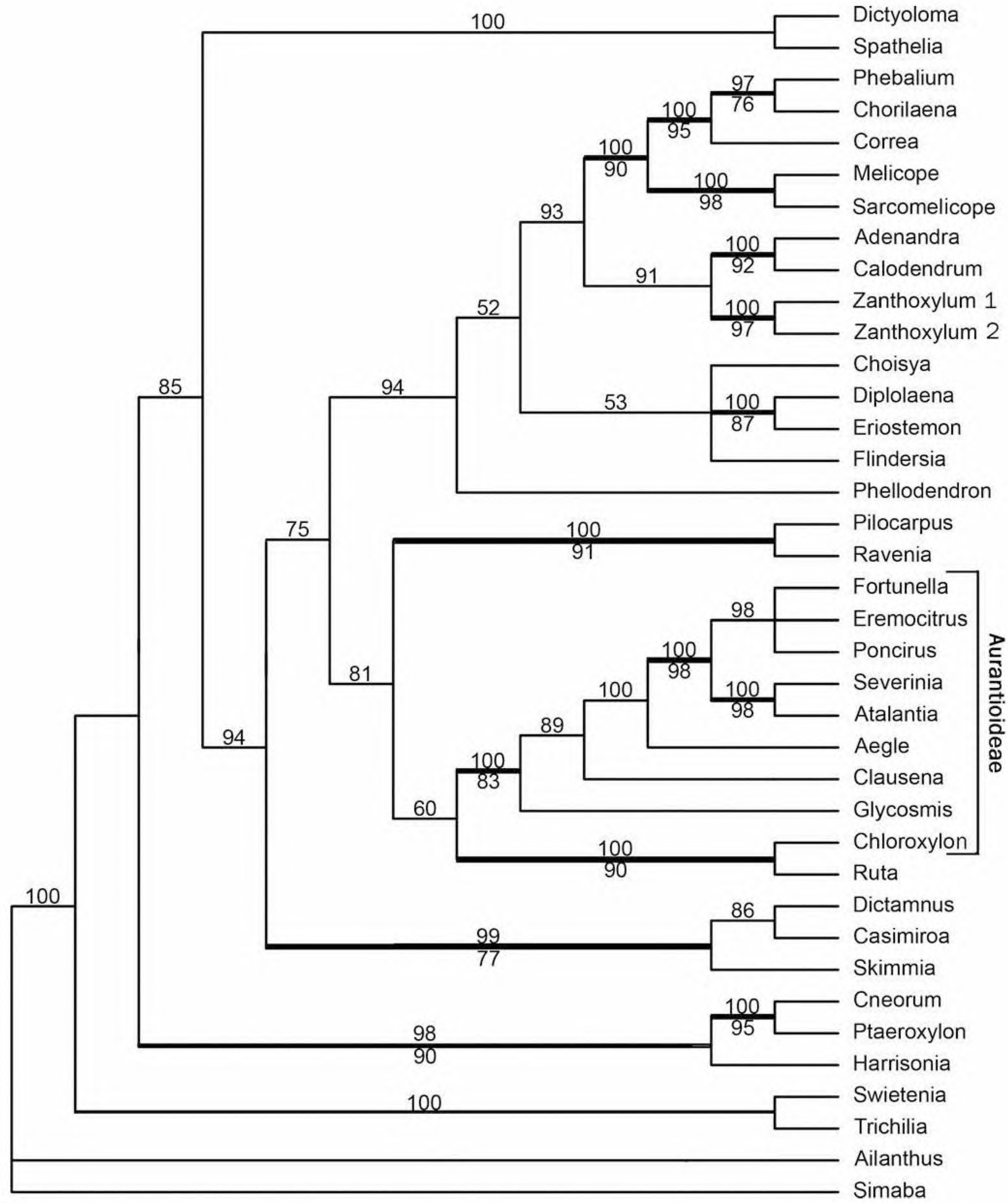


Figure 6. The majority rule consensus tree of 936 most-parsimonious trees (length = 1863 steps, CI = 0.59, RI = 0.58) obtained from the *Xdh* data from the Rutaceae. The bracket indicates the taxa belonging to subfamily Aurantioideae. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

were parsimony-informative. The analysis recovered 1654 equally optimal trees of 1380 steps (CI = 0.56, RI = 0.59; cf. Fig. 4 majority rule tree).

The Rutaceae s.l. were monophyletic but not supported in the strict consensus. Basal within the majority rule tree, the Rutaceae s.l. clade was the clade ((*Cneorum pulverulentum*, Cneoraceae + *Ptaeroxylon obliquum*, Ptaeroxylaceae; BS 100%) + *Harrisonia perforata*, Simaroubaceae; BS 80%). The next well-supported clade was (*Dictyoloma vandellianum* + *Spathelia excelsa*; BS 98%). The rest of the family (BS 87%) consisted of small clades that contain bootstrap support greater than 75%. Starting from the base of the clade, these included: (1) a clade containing members of the subfamily Aurantioideae (BS 98%) with (*Severinia buxifolia* + *Atalantia ceylanica*; BS 100%) and (*Eremocitrus glauca*, *Poncirus trifoliata* (L.) Raf., and *Glycosmis penta-*

phylla (Retz.) DC., *Murraya paniculata* (L.) Jack; BS 81%) internally supported; (2) a clade consisting of (*Chloroxylon swietenia* + *Ruta graveolens*; BS 76%) which is sister to the subfamily Aurantioideae clade (BS 75%); (3) a clade containing two species of *Zanthoxylum* (BS 74%); and (4) a clade containing ((*Melicope ternata* + *Sarcomelicope simplicifolia*; BS 100%) sister to a clade containing *Phebalium woombye*, *Diplolaena dampieri*, and *Correa pulchella* (BS 88%)).

RPS16

Approximately 36 gaps were required for proper alignment of the 38 sequences (*Phebalium* Vent. and *Harrisonia* not sequenced) of *rps16*. These gaps ranged from one to 14 bps. None of these gaps were parsimony-informative. Mean percentage G + C content is 34%. Of the 1054 positions constituting the aligned 38 sequences, 777 (74%) were variable and 479 (45%) were parsimony-informative. The analysis recovered 2172 equally optimal trees of 1643 steps (CI = 0.59, RI = 0.52; cf. Fig. 5).

The Rutaceae s.l. were monophyletic in the strict consensus tree. Within the majority rule tree, only five clades contained bootstrap support greater than 75%: (1) the clade containing exemplars of subfamily Aurantioideae (BS 87%); (2) the (*Severinia buxifolia* + *Atalantia ceylanica*; BS 98%) clade; (3) the clade containing two species of *Zanthoxylum* (BS 97%) sister to *Phellodendron amurense* Rupr. (BS 76%); and (4) the (*Melicope ternata* + *Sarcomelicope simplicifolia*; BS 97%) clade.

XDH

Approximately four gaps were required for proper alignment of the 38 sequences (*Murraya* J. Koenig ex L. and *Lunasia* not sequenced). These gaps ranged from one to 11 bps. None of these gaps were parsimony-informative. Mean percentage G + C content was 40%. Of the 1274 positions constituting the aligned 38 sequences, 747 (59%) were variable and 462 (36%) were parsimony-informative. The analysis recovered 936 equally optimal trees of 1863 steps (CI = 0.59, RI = 0.58; cf. Fig. 6).

The Rutaceae s.l. were monophyletic in the majority rule consensus tree. Within the tree, a number of clades contained bootstrap support greater than 75%, which include: (1) the (*Cneorum pulverulentum*, Cneoraceae + *Ptaeroxylon obliquum*, Ptaeroxylaceae; BS 95%) clade sister to *Harrisonia perforata*, Simaroubaceae (BS 90%); (2) the (*Dictamnus albus*, *Casimiroa edulis*, and *Skimmia anquetilia*; BS 77%) clade; (3) the clade containing members of the subfamily Aurantioideae (BS 83%) ((*Severinia buxifolia* + *Atalantia ceylanica*; BS 98%) clade sister to (*Fortunella polyandra*, *Eremocitrus glauca*, and *Poncirus trifoliata*; BS 98%); (4) the clade containing (*Chloroxylon swietenia* + *Ruta graveolens*; BS 90%); (5) the (*Pilocarpus pennatifolius* Lem. + *Ravenia infelix* Vell.; BS 91%) clade; (6) the (*Diplolaena dampieri* + *Eriostemon angustifolius*; BS 87%) clade; (7) the (*Adenandra uniflora* (L.) Willd. + *Calodendrum capense* Thunb.; BS 92%) clade; (8) the clade containing two species of *Zanthoxylum* (BS 97%); and (9) the well-supported clade (BS 90%) comprised of (*Melicope ternata* + *Sarcomelicope simplicifolia*; BS 98%) sister to the ((*Phebalium woombye* + *Chorilaena quercifolia*; BS 76%) + *Correa pulchella*; BS 95%) clade.

Combined analysis

Following the methods outlined by Mason-Gamer and Kellogg (1996) and recently applied by Eldenäs and Linder (2000), the data sets were considered combinable. Several nodes shared between the independent trees with bootstrap support greater than 75% included: *Cneorum pulverulentum* + *Ptaeroxylon obliquum*; *Dictyoloma vandellianum* + *Spathelia excelsa*; *Melicope ternata* + *Sarcomelicope simplicifolia*; *Severinia buxifolia* + *Atalantia ceylanica*; *Chloroxylon swietenia* + *Ruta graveolens*; the Aurantioideae clade; the clade (*Dictamnus albus*, *Skimmia anquetilia*, and *Casimiroa edulis*); two species of *Zanthoxylum*; and *Adenandra uniflora* + *Calodendrum capense*. Among the trees only one potentially conflicting node exists with bootstrap support greater than 75%, and this was the *Phebalium woombye–Diplolaena dampieri* clade. Among the independent analyses, the grouping of taxa within this clade has varied to include: *Phebalium woombye* + *Diplolaena dampieri* in the *rbcL*; *Phebalium woombye*, *Chorilaena quercifolia*, *Diplolaena dampieri*, *Eriostemon angustifolius*, and *Correa pulchella* in the *atpB*; *Diplolaena dampieri*, *Eriostemon angustifolius*, *Chorilaena quercifolia* in the spacer; *Phebalium woombye*, *Chorilaena quercifolia*, and *Correa pulchella* in the *Xdh*. The conflict appeared to be due to a lack of resolution or missing taxa; therefore, congruence existed between the data sets and a combined analysis was completed.

Multiple sequence alignment from exemplars from the Rutaceae and all outgroups resulted in a matrix of 7240 characters, of which (46%) included at least one accession with a gap. Mean percentage G + C content is 39%. Of the 7240 positions constituting the aligned sequences, 3259 (45%) were variable and

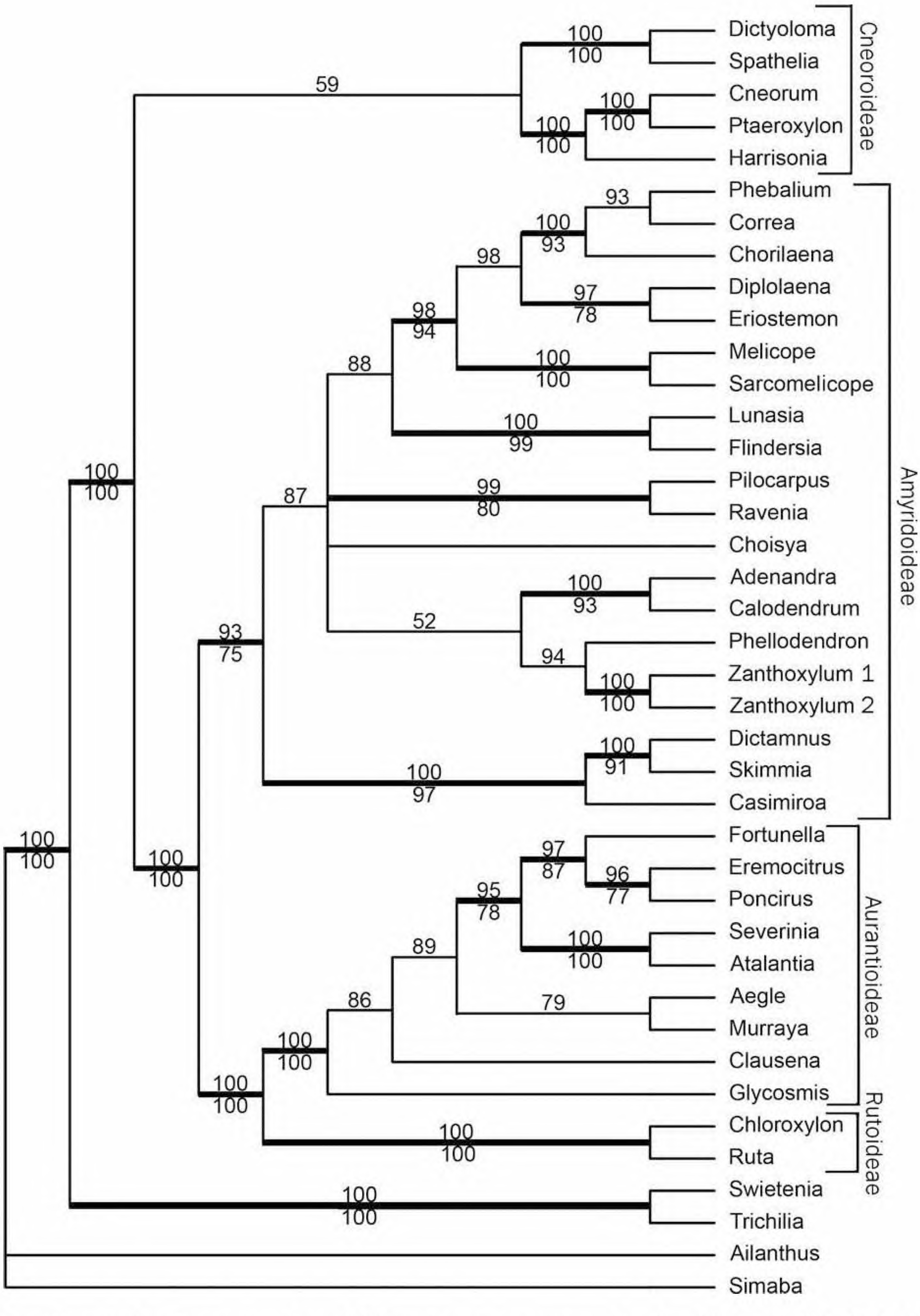


Figure 7. The majority rule consensus tree of 126 most-parsimonious trees (length = 6295 steps, CI = 0.48, RI = 0.54) obtained from the total data from the Rutaceae. Brackets indicate the taxa belonging to the four subfamilies. Numbers above the branches indicate consensus values; numbers below the branches are bootstrap values for nodes with more than 75% support.

1872 (26%) were parsimony-informative. The analysis recovered 126 equally optimal trees of 6295 steps (CI = 0.48, RI = 0.54; cf. Fig. 7).

The Meliaceae were a sister clade to the Rutaceae s.l. (BS 100%). The Rutaceae s.l. were supported as monophyletic in the strict consensus trees. Within the majority rule tree, most clades contain bootstrap support greater than 75%. These include: (1) the strongly supported (BS 100%) clade ((*Cneorum* + *Ptaeroxylon*) + *Harrisonia*); (2) a clade containing (*Dictyoloma vandellianum*, subfamily Dictyolomatoideae + *Spathelia excelsa*, subfamily Spathelioideae; BS 100%); (3) a clade containing members of the subfamily Aurantioideae (BS 100%) (*Severinia* +

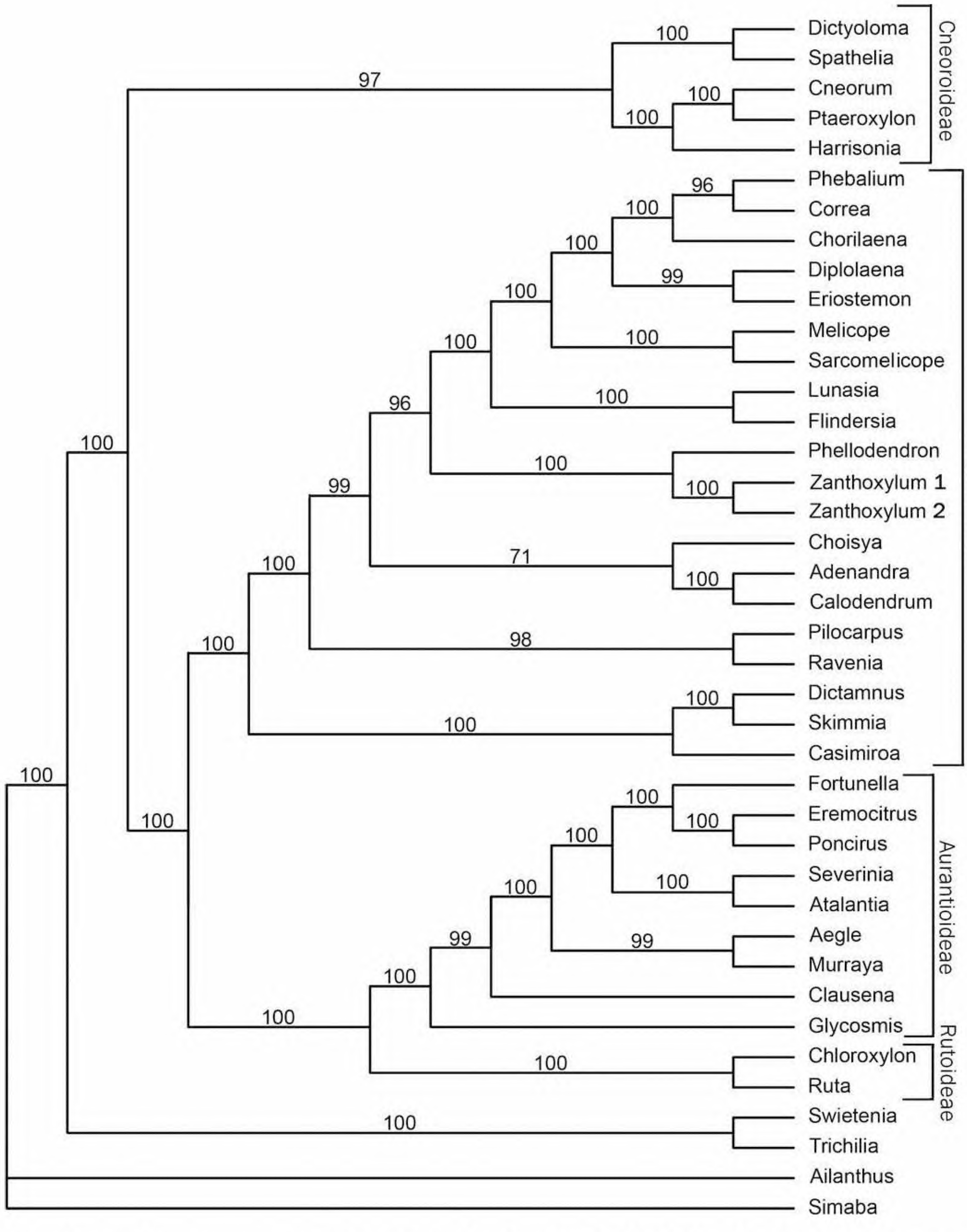


Figure 8. The Bayesian consensus tree from the combined of cpDNA and nrDNA analysis. Brackets indicate the taxa belonging to the four subfamilies. Numbers above nodes are posterior probability values.

Atalantia) + (*Fortunella* + (*Eremocitrus* + *Poncirus*; BS 77%) BS 87%). Basal to the subfamily Aurantioideae was the clade (*Chloroxylon swietenia* + *Ruta graveolens*; BS 100%); (4) a clade comprised of ((*Dictamnus albus* + *Skimmia anquetilia*; BS 91%) + *Casimiroa edulis*; BS 97%); (5) a clade containing (*Adenandra uniflora* + *Calodendrum capense*; BS 93%); (6) a clade containing two species of *Zanthoxylum* (BS 100%); (7) a clade containing (*Pilocarpus pennatifolius* + *Ravenia infelix*; BS 84%); (8) a clade consisting of (*Lunasia amara* + *Flindersia australis*; BS 99%); and (9) a well-supported clade (BS 94%) containing ((*Melicope* + *Sarcomelicope*; BS 100%) + ((*Phebalium*, *Correa*) + *Chorilaena*; BS 93%) + (*Diplolaena* + *Eriostemon*; BS 78%)).

Table 3. Summary of the results from separate and combined analyses of the *rbcL*, *atpB*, *atpB–bcL*, *trnL–trnF*, *rps16*, and *Xdh* region of Rutaceae.

Results	*rbcL*	*atpB*	*atpB–rbcL*	*trnL–trnF*	*rps16*	*Xdh*	Total
Total no. characters	1410	1489	987	1039	1054	1274	7240
No. variable characters (uninformative)	307	292	452	612	777	747	3259
No. parsimony-informative characters	157	153	222	427	479	462	1872
No. trees	18,352	9763	73,552	1654	2172	936	126
Tree length (steps)	406	353	657	1380	1643	1863	6295
Consistency index (CI)	50	53	53	56	59	59	48
Retention index (RI)	68	72	65	59	52	58	54
Clades with < 75% bootstrap values	7	9	6	12	5	15	22

In the Bayesian combined analysis, the group of exemplars from the Rutaceae were monophyletic with good posterior probability values (100%; Fig. 8). In all but one branch, the posterior probability values were higher than 96%. The only difference between the majority rule tree and the Bayesian tree was the sister group of *Adenandra uniflora* + *Calodendrum capense*. In the Bayesian analysis, *Choisya mollis* Standl. grouped with *Adenandra uniflora* + *Calodendrum capense* (posterior probability value 71%), whereas in the majority rule tree, *Adenandra uniflora* + *Calodendrum capense* formed a sister group with *Phellodendron amurense* and *Zanthoxylum* with very low support.

Discussion

Classification of the Rutaceae has suffered from incomplete studies. To date, morphological data have provided very few clues to the true relationships of this large group of plants. Molecular data have provided some information; however, more evidence was needed to have a well-supported phylogeny. During the review of this paper, another treatment based on morphological features was published (Kubitzki et al., 2011). The Kubitzki et al. (2011) treatment recognizes three subfamilies, Cneoroideae, Rutoideae, and Aurantioideae, and differs from this study. In the current comprehensive study of the Rutaceae, molecular data and selected morphological characters were used to reclassify the subfamilies of this economically important group of plants.

Sequence diversification

The *rps16* sequences produced the most parsimony-informative characters for similar taxon sampling when compared with the other chloroplast or nuclear regions: *rbcL* (157), *atpB* (153), *atpB–rbcL* (222), *trnL-–trnF* (427), *rps16* (479), and *Xdh* (462) (see Table 3). The *atpB* gene produced the fewest parsimony-informative characters. The *Xdh* gene had the highest number of resolved nodes at or above 75% bootstrap support when compared with all other genes from the chloroplast regions: *rbcL* (7), *atpB* (9), *atpB–rbcL* (6), *trnL–trnF* (12), *rps16* (5), and *Xdh* (15) (see Table 3). Although the *rsp16* gene had the highest number of informative characters, it had the fewest nodes at or above 75% bootstrap support, indicating that the informative characters were clustering at only a few nodes. The *Xdh*, with almost the same number of informative characters, had the highest number of nodes at or above 75% bootstrap support. The combined parsimony analysis had 22 nodes at or above 75% bootstrap support, whereas in the Bayesian analyses all but one branch had posterior probability values higher than 96%. Because of the large number of nucleotide characters from the chloroplast and nuclear regions included in this study as well as the high levels of resolution and support from both parsimony and Bayesian analyses, the results were sufficiently robust to justify a reclassification at the subfamily level.

Subfamily classification for the Rutaceae

The subfamily classification proposed here requires major rearrangements: (1) the taxa of the subfamily Aurantioideae remain the same; (2) subfamily Cneoroideae encompass the subfamilies Spathelioideae, Dictyolomatoideae, *Harrisonia* of the Simaroubaceae, *Cneorum* of the Cneoraceae and *Ptaeroxylon* of the family Ptaeroxylaceae; (3) subfamily Rutoideae include *Ruta* and *Chloroxylon* of subfamily Flindersioideae; and (4) subfamily Amyridoideae Link unite *Flindersia* of subfamily Flindersioideae with subfamily Toddalioideae and taxa previously included in subfamily Rutoideae.

Taxonomic Treatment

Rutaceae Juss.

I. Rutaceae subfam. **Aurantioideae** Horan., Char. Ess. Reg. Veg., 203. 1847, as "Aurantiaceae." Aurantiaceae Juss., Gen. Pl. 259. 1789. Auran-

tiales Link, Handbuch 2: 345. 1829. Aurantieae Rchb., Fl. Germ. Excurs. 2(2): 840. 1832. Aurantiineae Rchb., Deut. Bot. Herb.-Buch, 88. 1841. TYPE: *Aurantium* Tourn. ex Mill.

Included genera (9). *Aegle* Corrêa, *Atalantia* Corrêa, *Clausena* Burm. f., *Eremocitrus* Swingle, *Fortunella* Swingle, *Glycosmis* Corrêa, *Murraya* L. Jack, *Poncirus* Raf., and *Severinia* Ten ex Endl.

The subfamily Aurantioideae comprise a strongly supported monophyletic group. This confirmed what has been found in previous phylogenetic studies (Chase et al., 1999; Scott et al., 2000; Samuel et al., 2001; Morton et al., 2003; Poon et al., 2007; Gruppo et al., 2008; Bayer et al., 2009; Morton, 2009). Morton (2009) examined 20 non-molecular characters, including vegetative, floral, biochemical, and chromosomal features and found only one character, the basic chromosome number of $x = 9$, provided a synapomorphy for the subfamily. Many of the morphological characters (e.g., flowers white, fruit with pulp vesicles) that had been used to define the subfamily previouly proved to be homoplasious. Morton (2009) confirmed the need for new morphological characters providing synapormorphies for classification at the subfamilial level. Other characters more recently suggested as potential subfamilial characters, such as the presence of coumarins, were homoplasious. Many of the characters traditionally used to describe subfamily Aurantioideae, such as seeds without endosperm, could not be used in a cladistic analysis because of the lack of information and plant material.

Bayer et al. (2009) and Morton (2009) found that the two tribes Clausenesae Wight & Arn. and Citreae Meisn. were not monophyletic but could be if *Murraya* and *Merrillia* Swingle were moved to the Citreae. Bayer et al. (2009) also found that none of the subtribes of Citreae are monophyletic, and before further taxonomic subtribal classification could be established, more molecular work is needed for a well-supported topology and classification. Relationships among species and genera, or groups, are complicated by several factors such as a long history of cultivation and wide cross-compatibility among species (Mabberley, 2004).

II. Rutaceae subfam. **Cneoroideae** Webb, London J. Bot. 1: 257. 1842. Cneoraceae Vest, Anleit. Stud. Bot. 267, 285. 1818. Cneorales Link, Handbuch 2: 440. 1829. Cneoreae Baill., Hist. Pl. 4: 431, 503. 1873. TYPE: *Cneorum* L.

Included genera (5). *Cneorum* L., *Dictyoloma* A. Juss., *Harrisonia* R. Br. ex A. Juss., *Ptaeroxylon* Eckl. & Zeyh., *Spathelia* L.

Within the parsimony analysis, both the pairing of *Dictyoloma* and *Spathelia* and the clade that included *Cneorum*, *Ptaeroxylon*, and *Harrisonia* (formerly Simaroubaceae) was strongly supported; however, the support of the sister relationship between these clades was weak. Within the Bayesian analyses, all of these clades had over 96% posterior probabilities. A synapomorphy for subfamily Cneoroideae is the presence of compounds known as rutacean chromones. Species of *Harrisonia*, *Spathelia*, and *Cneorum* all produce limonoids and ptaeroxylin chromones (Taylor, 1982, 1983; Da Silva & Gottlieb, 1987; Vieira et al., 1988, 1990), whereas *Ptaeroxylon* produces these chromones but no limonoids (Waterman, 1983). This relationship was also strongly supported in the studies by Chase et al. (1999) and Gruppo et al. (2008). Of the three applicable subfamily names, the subfamily Cneoroideae Webb (including *Cedrelopsis* Baill., *Harrisonia*, and *Ptaeroxylon*) was established in 1842, whereas Dictylomatoidae Engl. and Spatheloiodeae Engl. were described in 1896; therefore, the name Cneoroideae has priority over the other two names at subfamily rank.

III. Rutaceae subfam. **Rutoideae** Arn., Botany 104. 1832. Rutaceae Juss., Gen. Pl. 296. 1789. Rutales Juss. ex Bercht. & J. Presl, Přir. Rostlin 220. 1820. Ruteae Juss. in Dumortier, Anal. Fam. Pl. 45. 1829. TYPE: *Ruta* L.

Included genera (2). *Chloroxylon* DC., *Ruta* L.

Only two genera belong to the subfamily Rutoideae; the relationship of *Ruta* and *Chloroxylon* was strongly supported in both the parsimony and the Bayesian analyses. These genera have a strong synapomorphy of a base chromosome number of $x = 10$ (Stace et al., 1993). This base number has only been found in *Ruta*, *Chloroxylon*, and *Boenninghausenia*. Preliminary molecular data indicate that these three genera form a well-supported group (Morton, unpub.). This *Ruta* and *Chloroxylon* grouping has been found in several other studies that used different vouchered samples, representing different populations from different localities (Chase et al., 1999; Morton et al., 2003; Poon et al., 2007; Gruppo et al., 2008; Bayer et al., 2009; Morton, 2009).

IV. Rutaceae subfam. **Amyridoideae** Link, Handbuch 2: 128. Jan.–Aug. 1831. Amyridaceae Kunth, Ann. Sci. Nat. (Paris), 2: 353. 1824. Amyrideae DC., Prodr. 2: 81. 1825. Amyridales J. Presl, Nowočeská Bibl. 7: 335. 1846. Amyridineae Engl., Engler & Prantl, Nat.

Pflanzenfam. Teil III, Abt. 4–5: 111, 181. 1896. TYPE: *Amyris* P. Browne.

Included genera (19). *Adenandra* Willd., *Calodendrum* Thunb., *Casimiroa* La Llave, *Choisya* Kunth, *Chorilaena* Endl., *Correa* Andrews, *Dictamnus* L., *Diplolaena* R. Br., *Eriostemon* Sm., *Flindersia* R. Br., *Lunasia* Blanco, *Melicope* J. R. Forst. & G. Forst., *Phebalium* Vent., *Phellodendron* Rupr., *Pilocarpus* Vahl, *Ravenia* Vell., *Sarcomelicope* Engl., *Skimmia* Thunb., *Zanthoxylum* L.

The subfamily Amyridoideae consist of all the genera of subfamily Rutoideae (except *Ruta*), *Flindersia* (type for subfamily Flindersioideae, Handb. Syst. Bot. 2: 681. 1881, as "Flindersieae"), and the genera of subfamily Toddalioideae. These results support the conclusions of Gadek et al. (1996), Chase et al. (1999), Poon et al. (2007), and Gruppo et al. (2008), who stated that the subfamilies Toddalioideae and Rutoideae must be unified into one subfamily. The oldest subfamily name that excludes the genus *Ruta* is subfamily Amyridoideae published in 1831 and, therefore, by priority is the name to use for this group of genera. Traditionally, Engler (1931) separated subfamily Toddalioideae from subfamily Rutoideae by fruit characters. However, revisionary studies by Hartley (1974, 1981, 1982) indicated that genera of subfamily Toddalioideae with syncarpous, drupaceous fruits are more closely related to genera of subfamily Rutoideae with apocarpous or subapocarpous follicular fruits. A study of ovule and seed-coat patterns found little distinction between the two subfamilies (Boesewinkel, 1980). While biochemical studies by Fish and Waterman (1973) and later by Da Silva et al. (1988) provided some evidence of a link between the subfamilies Rutoideae and Toddalioideae, to date there are no morphological, anatomical, or biochemical synapomorphies for the union of the two subfamilies. Additional molecular and morphological work is needed to resolve relationships among subfamily Amyridoideae. Gruppo et al. (2008) suggested that this clade appeared to be correlated with the geographic distribution of the groups, although this pattern was not clear in this analysis. The Old World taxa appear to be interdigitated with taxa of the New World. The grouping of *Dictamnus* with *Casimiroa* and *Skimmia* as a clade was also found by Chase et al. (1999) and by Gruppo et al. (2008), although no morphological or biochemical characters supported this grouping. The clade consisting of *Zanthoxylum* and *Phellodendron* was also found in a study by Chase et al. (1999, *atpB* clade) and by Poon et al. (2007), with support by one character of 1-BT1Q alkaloids (Waterman, 1975).

Conclusion and Future Plans

Four subfamilies, all monophyletic, are now recognized within the Rutaceae: (1) subfamily Aurantioideae, (2) subfamily Cneoroideae, (3) subfamily Rutoideae, and (4) subfamily Amyridoideae. Within these four subfamilies, resolution and good bootstrap support and posterior probability values are recovered for many of the clades. The most significant phylogenetic ambiguities remain in the subfamily Amyridoideae, from which only 19 of the approximately 120 genera have been sampled. To address these problems and to further consolidate results, the author plans to expand the taxon sample to include more genera within subfamily Amyridoideae. The author is confident that the relationships presented here will be further supported by the addition of new data and that these revised subfamily circumscriptions represent significant steps toward a natural and stable classification that will stand the test of time and aid additional studies of these diverse and important taxa.

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FIELD GUIDE TO THE CULTIVATED EUCALYPTS (MYRTACEAE) AND HOW TO IDENTIFY THEM[1]

Matt Ritter[2]

Abstract

This paper provides identification keys that are based entirely on morphological features to commonly and widely cultivated eucalypts, encompassing *Eucalyptus* L'Hér., *Angophora* Cav., and *Corymbia* K. D. Hill & L. A. S. Johnson in the Myrtaceae Juss. The key includes 173 taxa: one species of *Angophora*, nine species of *Corymbia*, and 163 species of *Eucalyptus*. Evidence for cultivation was determined by accounts in the literature, herbaria, personal communications, and observations of living trees in cultivation in Europe, North America, Africa, and Australia. The locations, prevalence of cultivation, and naturalization of several eucalypt species are discussed.

Key words: *Angophora*, *Corymbia*, eucalypt, *Eucalyptus*, Myrtaceae.

In 1774, at the Royal Botanic Gardens at Kew, England, the messmate (*Eucalyptus obliqua* L'Hér.) became the first cultivated eucalypt. Since that time, hundreds of species have been introduced into cultivation in temperate, tropical, and subtropical countries worldwide. Eucalypts are now second only to the pines as the most extensively planted trees in the world. They are grown for lumber, paper pulp, pilings and posts, fuel wood, medicinal products, tannins, oils, and as windbreaks and ornamentals. More than 150 of the approximately 900 eucalypts are regularly and widely grown (McClatchie, 1902; Boland et al., 1980; Wrigley & Fagg, 2010). In many countries where cultivated eucalypts have become prominent features of the landscape, they are admired for their many uses and aesthetic value while at the same time demonized as foreign invaders, and over 70 species have been observed reproducing on their own outside cultivation (Hussey et al., 1997; Forsyth et al., 2004; Ritter & Yost, 2009; Rejmánek & Richardson, 2011a).

In the current, most widely accepted classification, the eucalypts constitute three genera: *Angophora* Cav. with 10 species, *Corymbia* K. D. Hill & L. A. S. Johnson with 95 species, and *Eucalyptus* L'Hér. with approximately 760 species (Slee et al., 2006). *Angophora* was segregated from *Eucalyptus* by Cavanilles (1797) on the basis of the opposite adult leaves, presence of sepals, and absence of an operculum (bud cap or fused perianth). Nearly 200 years later, two Australian botanists, Kenneth Hill and Lawrence Johnson, combined two *Eucalyptus* subgenera, *Blakella* L. D. Pryor & L. A. S. Johnson ex Brooker and *Corymbia* (K. D. Hill & L. A. S. Johnson) Brooker (bloodwoods, ghost gums, and spotted gums), and described the new genus *Corymbia* (Pryor & Johnson, 1971; Hill & Johnson, 1995). This taxonomy was corroborated by molecular phylogenetic work, revealing that *Corymbia* is more closely related to *Angophora* than to *Eucalyptus* (Ladiges et al., 1995; Udovicic et al., 1995; Steane et al., 2002). Subsequently, Brooker (2000) proposed a less widely accepted taxonomic scheme with one genus, *Eucalyptus*, divided into seven subgenera, including *Corymbia* and *Angophora*. In general, *Corymbia* can be distinguished from *Eucalyptus* by the presence of discolorous leaves (abaxially lighter), terminal inflorescences, and large, urn-shaped fruits. Unfortunately, there are species of *Corymbia* that lack one or more of these easily recognized characteristics and several species of *Eucalyptus* that exhibit them.

Eucalypts are cultivated in all tropical, subtropical, and Mediterranean climate areas of the world. Although they were initially grown as horticultural oddities, foresters quickly discovered their potential as commercial plantation trees. Social engineers, planners, and entrepreneurs have promoted worldwide eucalypt planting for the last 150 years because of their many valuable characteristics—they are

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readily propagated from seed, grow fast, thrive in degraded soils and dry climates, can sustain regular coppicing, and are generally pest free. Between 10 and 20 species are widely grown in large plantations destined for use in paper pulp and other forestry products, whereas hundreds of others are grown for honey production, for shade, and as windbreaks and ornamentals. The most commonly grown species are *Eucalyptus globulus* Labill. (primarily in Australia, Central and South America, California, Spain, and Portugal), *E. grandis* W. Hill and hybrids between *E. grandis* and *E. urophylla* S. T. Blake (primarily in wetter areas including Brazil, Uruguay, Hawaii, China, South Africa, Congo, Zimbabwe, and Southeastern Asian countries), and *E. camaldulensis* Dehnh. (primarily in more arid areas of Africa, western North America, Peru, and the Mediterranean sea basin). More than half of the approximately 20 million hectares under eucalypt cultivation are in India (20% of total cultivated area), Brazil (19%), and China (13%) (Wang & Brooker, 1991; Florence, 1996; Turnbull, 1999; Cossalter & Pye-Smith, 2003; Iglesias-Trabado & Wilstermann, 2009; FAO, 2010).

This long history of widespread eucalypt planting has resulted in several species becoming controversial in the regions where they are now conspicuous features of the landscape. Researchers continue to debate the effects of eucalypt plantations on the natural ecosystems, biodiversity, wildlife, and ecosystem services (Poore & Fries, 1985; Sax, 2002; Lindenmayer & Hobbs, 2004; Lockwood & Gilroy, 2004; Díaz-Balteiro & Rodríguez, 2006; Proença et al., 2010; Wang et al., 2011). In general, eucalypts are less successful at invading natural areas than are several species of pines (e.g., *Pinus radiata* D. Don and *P. pinaster* Besser), other tree species in the Myrtaceae (e.g., *Melaleuca* L. spp. and *Psidium* L. spp.), and tree species in the Fabaceae (e.g., species of *Acacia* Mill. and *Prosopis* L., *Leucaena leucocephala* (Lam.) de Wit, and *Robinia pseudoacacia* L.) (Bargali et al., 1993; Richardson, 1998; Pyšek et al., 2004; Mooney et al., 2005; Rejmánek & Richardson, 2011a, 2011b). Several hypotheses have been proposed for the poor performance of eucalypts as weeds, even though they are widely planted. Eucalypts have limited, short distance, wind-dispersed seeds; generally lack compatibility with soil mycorrhizal fungi; and exhibit low levels of seedling recruitment because of their small, exalbuminous seeds (Brooker & Kleinig, 1999, 2002, 2004; Williams & Woinarski, 1997; Pampolina et al., 2002; Díez, 2005; Forrester et al., 2006; Rejmánek & Richardson, 2011b).

Eucalypt identification, although crucial in many situations, is often difficult. This difficulty is exacerbated when the provenance of naturalized or cultivated trees is unknown. I present here an identification guide to the world's most widely grown eucalypts—a group of species that exhibit the gamut of diversity in the genus, with greatly varied bark, leaves, and reproductive structures. This identification key relies entirely on morphological characters (and not place of origin) and prioritizes nonreproductive structures that are perennially present. The correct identification of many species, however, will often require examination of flowers and fruit.

Materials and Methods

This study was based on the morphological analysis of living specimens of eucalypt species on several continents (Europe, North America, Africa, and Australia). Herbaria were visited, and vouchered specimens from cultivated and wild areas were used in morphological analysis for preparation of the key. Herbaria visited in which specimens were examined (cited, according to abbreviations from Holmgren et al., 1990) include: South Africa (BOL, CT, SAM), Hawaii (HAW, PTBG), Australia (BRI, MEL, KPBG, UWA), the continental United States (ASU, CAS, FTG, LA, OBI, SD, UC), and Europe (K, UNEX). Evidence for cultivation was determined by accounts in the literature, herbaria, personal communications, and observations of living trees.

Genus-level Description and Characters Important for Taxonomic Identification

The name *Eucalyptus* was originally published in 1788 by a French botanist living in London named Charles Louis L'Héritier de Brutelle in a description of plants growing at the Royal Botanic Garden at Kew. The genus name is derived from the Greek "eu," meaning "well," and "kalyptos," meaning "covered," referring to the bud cap or operculum (a fused perianth).

At maturity eucalypts become small to large trees (Fig. 1A–C), multistemmed small trees (mallees), or shrubs (Fig. 1D), sometimes with a fire-resistant basal burl or lignotuber (Fig. 2A). Their bark may be shedding, smooth to the ground or with rough bark persistent near the base, powdery to the touch, fibrous or hard, compacted, and rough to the smallest branches (Fig. 1E–I). Oil glands are usually present in the leaves (Fig. 2G, L, M) and sometimes present as a dark line or spots within the pith of smaller stems (Fig. 2C).

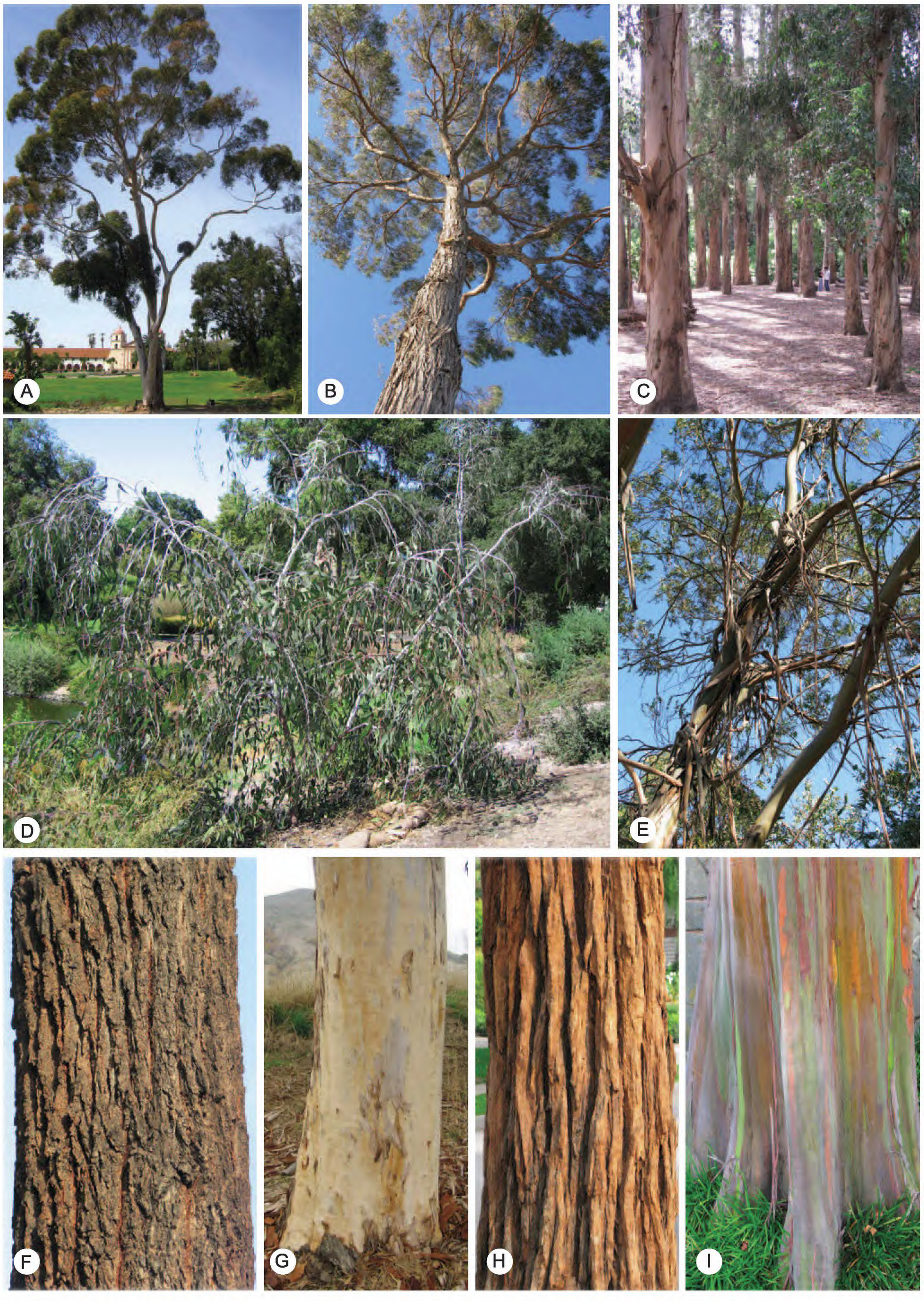


Figure 1. Growth forms and bark diversity in *Eucalyptus*. A–C, trees. —A. *Eucalyptus cladocalyx* F. Muell., showing typical tree form. —B. *Eucalyptus nicholii* Maiden & Blakely, with rough bark on trunk and small branches. —C. *Eucalyptus globulus* Labill., with smooth bark, sometimes with imperfectly shed rough bark on the basal area of trunk. —D. *Eucalyptus caesia* Benth., with multistemmed, shrubby mallee form. —E. *Eucalyptus parvula* L. A. S. Johnson & K. D. Hill, with bark shedding in long ribbons. —F. *Eucalyptus sideroxylon* A. Cunn. ex Woolls, showing typical ironbark trunk. —G. *Eucalyptus cladocalyx*, with bark shed in plates to the ground level. —H. *Eucalyptus robusta* Sm., showing rough, reddish brown bark. —I. *Eucalyptus deglupta* Blume, with smooth rainbow-colored bark to the ground level.

The leaves are of two different types in eucalypts. The juvenile leaves (leaves of seedlings, young plants, or new growth on mature plants after stems are cut or damaged) are generally attached oppositely, oriented horizontally, often sessile, heart-shaped or ovate to elliptical, clasping the stem, and glaucous (Fig. 2D). The adult leaves are generally attached alternately, hanging vertically, petiolate, linear to ovate, but most often lanceolate, and glossy or dull. Most often adult leaves are the same color on both sides, but many species have adult leaves that are discolorous and lighter on the underside (i.e., abaxially; Fig. 2F). Some species reproduce while the crown is in the juvenile leaf phase (Fig. 2E; see group 1 in the key for examples).

The inflorescences in eucalypts are unbranched umbels (sometimes condensed into heads) in leaf axils with three, seven, or more flowers (Fig. 2I), or highly branched, panicle-like clusters at branch tips (Fig. 2J) or in leaf axils, or rarely as solitary flowers in leaf axils. The peduncle can be round in cross-section (Fig. 3C) or flat and straplike (Fig 3F).

The outer floral organs (perianth) in eucalypts are sometimes fused into one or two opercula (bud caps), that are shed prior to or during flowering (Figs. 2N, 3A). A ring-shaped operculum scar on the developing bud is present when there are two opercula and the outer operculum is shed early in bud development (Fig. 2O, P). This operculum scar is absent when there is a single operculum or the outer operculum is held until near flowering (Fig. 3B). The operculum can be variously shaped, but most often it is beaked, conical, rounded, or horn-shaped (Fig. 3H). The stamens are numerous; in some species the outer stamens lack anthers (Fig. 3C, D); in others the stamens are in four clusters within the flower (Fig. 3G). The inferior ovary is sunken inside and fused with the hypanthium (Fig. 3E).

The fruit is a thick-walled, woody capsule that splits open at lines between three, four, or five valves at the top (Fig. 4). The hypanthium forms the hard outer layer; the pericarp is comparatively thin. After splitting open, the valves may be below the rim of the hypanthium (enclosed), exserted beyond the rim, or at the level of the rim (Fig. 4E). As the fruit develops, the hypanthium disk (the tissue between the ring where the stamens were attached and the top of the ovary) can be flat, ascending, or descending (Fig. 4F). Sometimes the valve tips remain fused across the fruit opening after dehiscence (Fig. 4C, H, *Eucalyptus cornuta* Labill. and *E. robusta* Sm., respectively). The fruit may be variously shaped at maturity (Fig. 4L). The seeds are generally 0.5 mm to 1.5 cm, cuboid or flattened, dark-brown or black, and surrounded by tan-colored, abundant chaff (unfertilized ovules) (Fig. 4K, *E. lansdowneana* F. Muell. & J. E. Br.).

Taxonomic Keys to Commonly and Widely Grown Eucalypts (*Angophora*, *Corymbia*, and *Eucalyptus*)

The following key to groups delineates the species treated here by easily recognized morphological characteristics. The nine species groupings are artificial, not based on any taxonomy or evolutionary relationships, and are used solely to make species identification easier. There is a description of the group and exemplar species for each group at the beginning of the key for each group. Several species appear in more than one group. *Eucalyptus* species occur in all group keys; *Angophora costata* is found in Key 3, and *Corymbia* species appear in Keys 3 and 4.

Key to Eucalypt Species Groups

1. Crown of mature reproductive tree made of mostly juvenile leaves; leaves mostly opposite, sessile, ovate, and glaucous ..... Group 1
1′. Crown of mature reproductive tree made of mostly adult leaves; leaves mostly alternate, sometimes opposite, clearly petiolate, lanceolate, and sometimes glaucous 2
2. Ironbarks, the bark rough, deeply furrowed, very hard (not easily pulled from tree), dark brown, gray, or black, retained on trunk and limbs ..... Group 2
2′. Not ironbarks, the bark smooth or rough, fibrous, shallowly furrowed, soft, brown to gray, retained on trunk and limbs or shedding in strips, plates, or sheets, leaving trunk smooth 3
3. Leaves discolorous, lighter on the underside (abaxial face) of leaves ..... Group 3
3′. Leaves concolorous, same color on both blade faces 4
4. Inflorescences compound, highly branched clusters at branch tips or in leaf axils ..... Group 4
4′. Inflorescences unbranched, single or paired umbels, or solitary flowers in leaf axils 5
5. Buds and fruits in clusters of 3 or solitary in leaf axils ..... Group 5
5′. Buds and fruits in clusters of more than 3 (usually 7 or more, some buds may be lost due to abortion or destruction) 6
6. Operculum scar absent from mature buds (buds have a single operculum with no circumferential scar on the bud surface caused by the shedding of the outer operculum, as happens in many other eucalypts); and buds and fruits usually in clusters of 11 or more; and disk of fruit level with rim, reddish brown, and shiny; and side leaf veins few, acutely angled, or parallel ..... Group 6

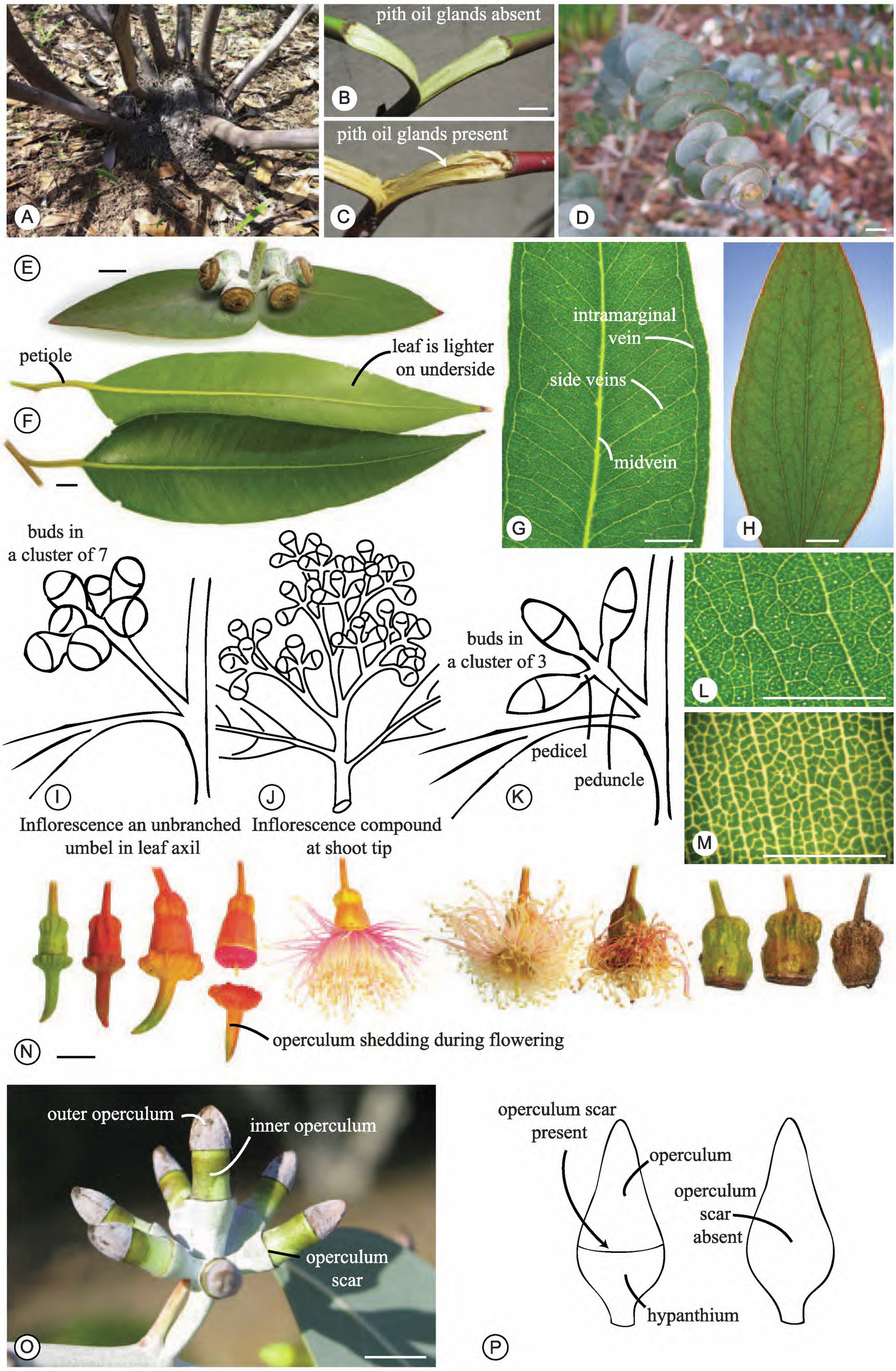


Figure 2. Lignotuber, pith, and leaf oil glands, as well as leaf and inflorescence characteristics in eucalypts. —A. Lignotuber of *Eucalyptus preissiana* Schauer. —B. Stem of *E. camaldulensis* Dehnh., without pith oil glands. —C. Stem of *E. torquata* Luehm., with pith oil glands. —D. Juvenile growth of *E. kruseana* F. Muell. —E. Opposite, sessile, juvenile leaves in the reproductive state, *E. cinerea* F. Muell. ex Benth. —F. Discolorous adult leaves in *E. robusta* Sm. —G. Typical eucalypt venation, with a midvein branching to side veins that converge near the leaf margin at the intramarginal vein, illustrated from *E. camaldulensis*. —H. Leaf venation, illustrating the prominently 3-veined characteristic, taken from *E. stellulata* Sieber ex DC.

6′. Operculum scar present on mature buds; buds and fruits in clusters of 7 or sometimes more; disk of fruit varying; side leaf veins varying 7
7. Peduncle broad, flattened, and straplike ..... Group 7
7′. Peduncle round or only slightly flattened in cross-section 8
8. Valves of mature fruit enclosed and sunken below fruit (hypanthium) rim or level with fruit rim ..... Group 8
8′. Valves of mature fruit clearly exserted beyond fruit rim ..... Group 9

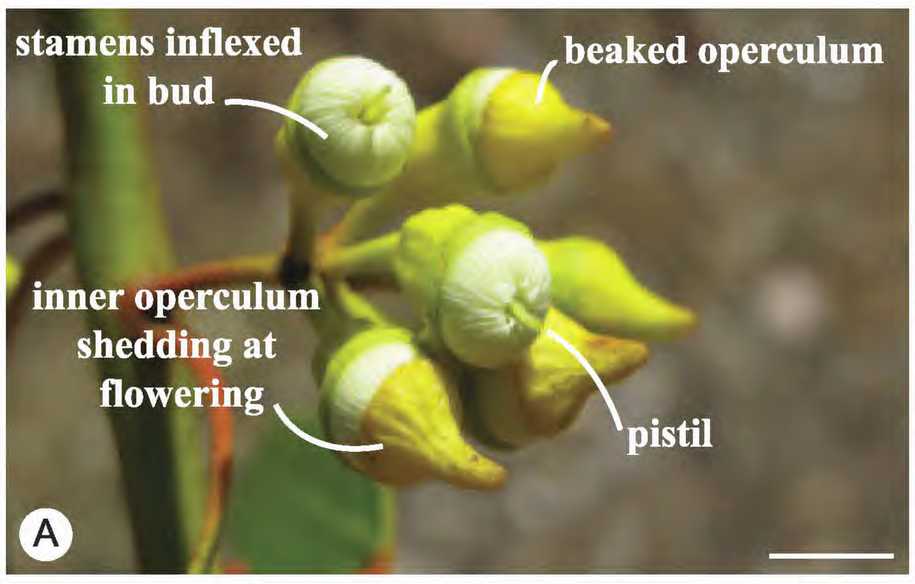
Group 1, Trees, Mallees, or Shrubs with a Crown of Mostly Juvenile Leaves

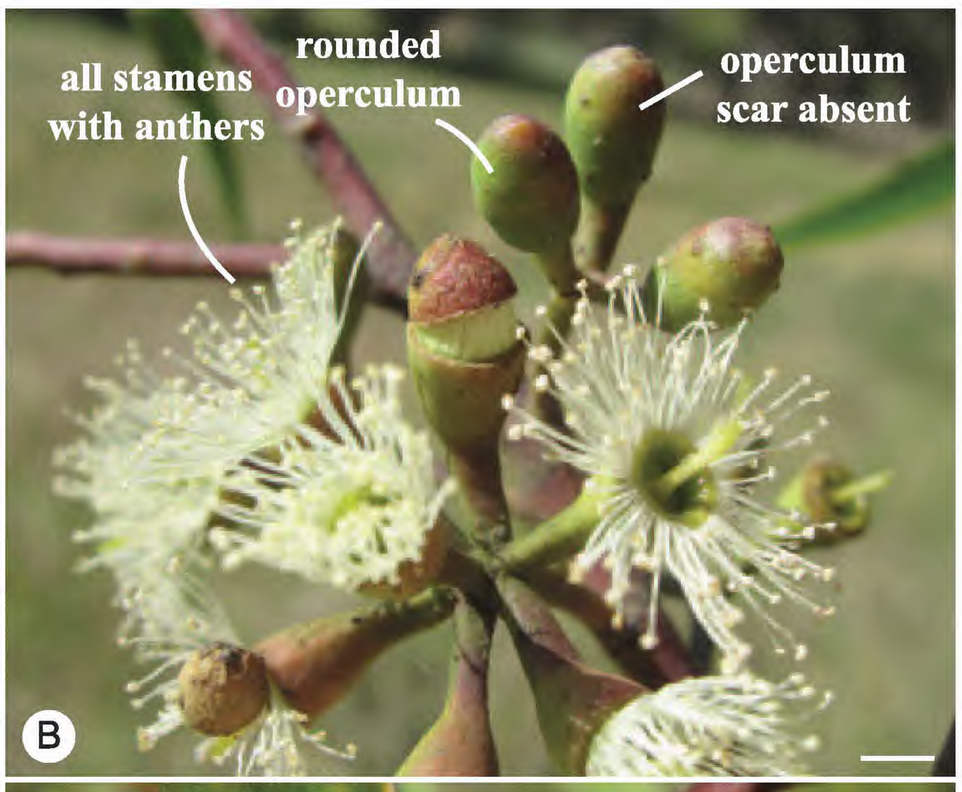
This group contains species in which the reproductively mature crown (branched, leafy canopy with flowers and fruits) is made primarily of leaves that are arrested in the juvenile leaf phase. The leaves are generally attached oppositely, oriented horizontally, often sessile, cordate or ovate, clasping the stem, and glaucous (Fig. 2D, E, *Eucalyptus kruseana* F. Muell. and *E. cinerea*, respectively). Mature growth forms are trees (*E. melanophloia* F. Muell.), mallees (*E. kruseana* F. Muell.), and shrubs (*E. macrocarpa* Hook.).

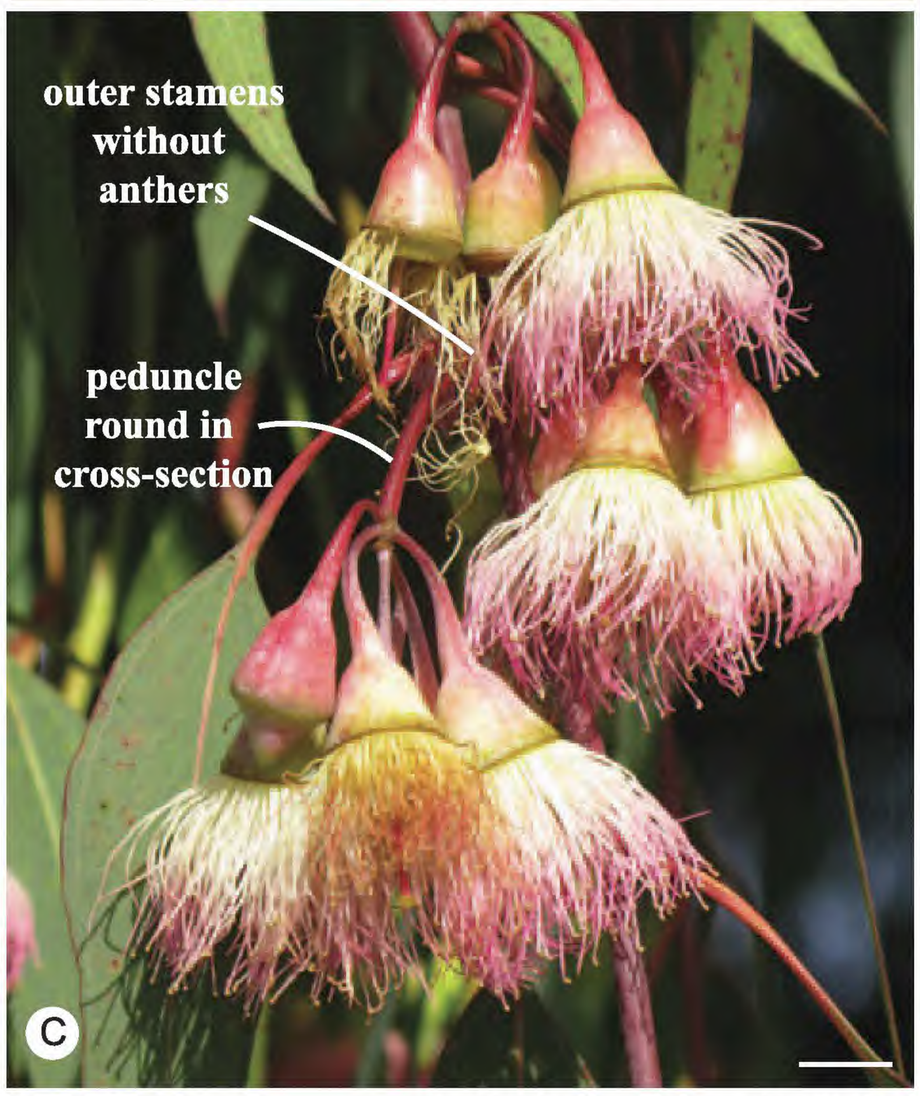
1. Most leaves fused at the base, forming a disk 2
2. Buds and fruits in clusters of 3 ..... *Eucalyptus perriniana* (spinning gum)
2′. Buds and fruits in clusters of 7 or more ..... *E. risdonii* (Risdon peppermint)
1′. All leaves free (not fused) 3
3. Ironbark, the bark rough, deeply furrowed, very hard (not easily pulled from tree), dark brown, gray, or black, retained on trunk and limbs ..... *E. melanophloia* (silver-leaved ironbark)
3′. Not ironbarks, the bark smooth or rough, fibrous, shallowly furrowed, soft, brown to gray, retained on trunk and limbs or shedding in strips, plates, or sheets, leaving trunk smooth 4
4. Mallees or multistemmed shrubs 5
5. Stems square in cross-section 6
6. Leaves sessile, inflorescences compound, at branch tips (terminal) ..... *E. pruinosa* (silver box, silverleaf box)
6′. Leaves petiolate and sessile, inflorescences unbranched umbels, in leaf axils 7
7. Buds pedicellate, in clusters of 3 ..... *E. pleurocarpa* (tallerack)
7′. Buds sessile, in clusters of 7 or more ..... *E. neglecta* (Omeo gum)
5′. Stems round in cross-section 8
8. Buds and fruits in clusters of more than 3 9
9. Leaves crowded on stem; flowers greenish yellow; fruit < 0.75 cm wide; valves at rim level ..... *E. kruseana* (bookleaf mallee)
9′. Leaves not crowded on stem; flowers pale yellow or whitish; fruit > 1 cm wide; valves exserted ..... *E. crucis* (Southern Cross silver mallee)
8′. Buds and fruits in clusters of 3 or solitary in leaf axils 10
10. Buds and fruits solitary in leaf axils 11
11. Buds and fruits pedicellate on downturned peduncles .... *E. rhodantha* (rose mallee)
11′. Buds and fruits sessile on erect, stout peduncles ..... *E. macrocarpa* (mottlecah)
10′. Buds and fruits in clusters of 3 12
12. Buds and fruits sessile; flowers white; fruit < 1.5 cm wide ..... *E. pulverulenta* (silver-leaved mountain gum)
12′. Buds and fruits pedicellate; flowers pink or red or pale yellow; fruit > 2 cm wide ..... *E. pyriformis* (Dowerin rose)
4′. Trees 13
13. Bark smooth, shedding, sometimes with imperfectly shed rough bark on basal area of trunk 14
14. Inflorescence pendulous, fruit urn-shaped ..... *E. urnigera* (urn gum)
14′. Inflorescence erect, fruit barrel- or cup-shaped 15
15. Some leaf margins crenulate; fruit 1 cm wide, sessile ... *E. cordata* (heart-leaved silver gum)
15′. All leaf margins entire; fruit < 1 cm wide, very shortly pedicellate .... *E. gunnii* (cider gum)
13′. Bark rough, furrowed, retained on trunk and limbs 16
16. Buds and fruits in clusters of 3 ..... *E. cinerea* (mealy stringybark, Argyle apple)
16′. Buds and fruits in clusters of more than 3 17
17. Leaf margins crenulate ..... *E. crenulata* (Buxton gum)
17′. Leaf margins entire 18

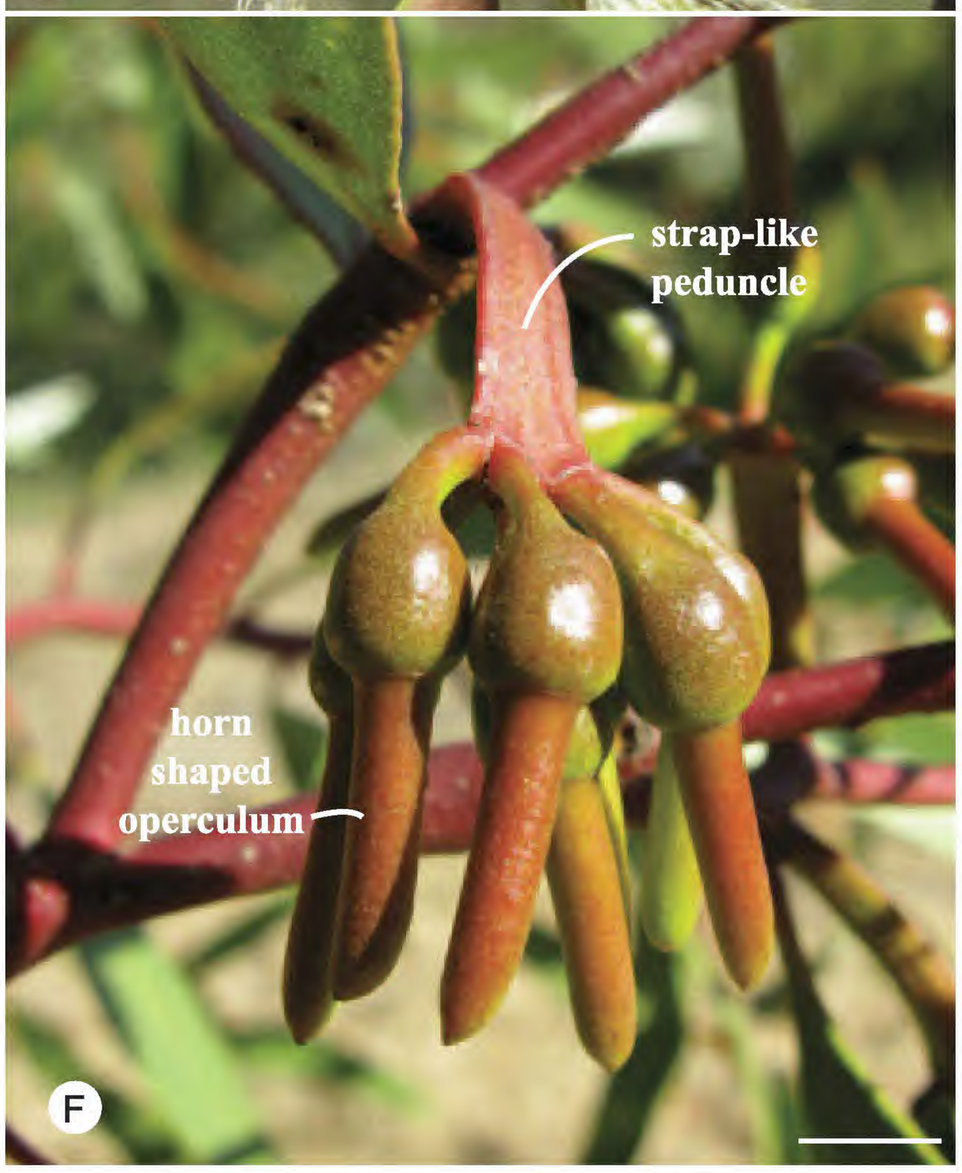
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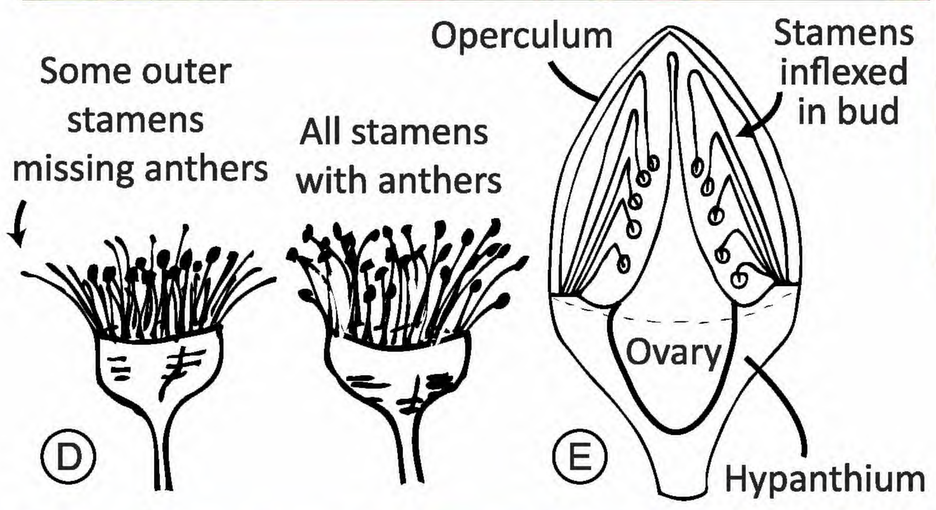
I–K. Inflorescence characteristics. —L. Typical leaf with oil glands, taken from *E. camaldulensis*. —M. Leaf lacking oil glands, taken from *Corymbia ficifolia* (F. Muell.) K. D. Hill & L. A. S. Johnson. —N. Developmental series of flowering and fruit formation in *E. torquata*. —O. Flower bud characteristics, taken from *E. prava* L. A. S. Johnson & K. D. Hill. —P. Flower bud and operculum terminology. A–O scale bars = 1 cm.

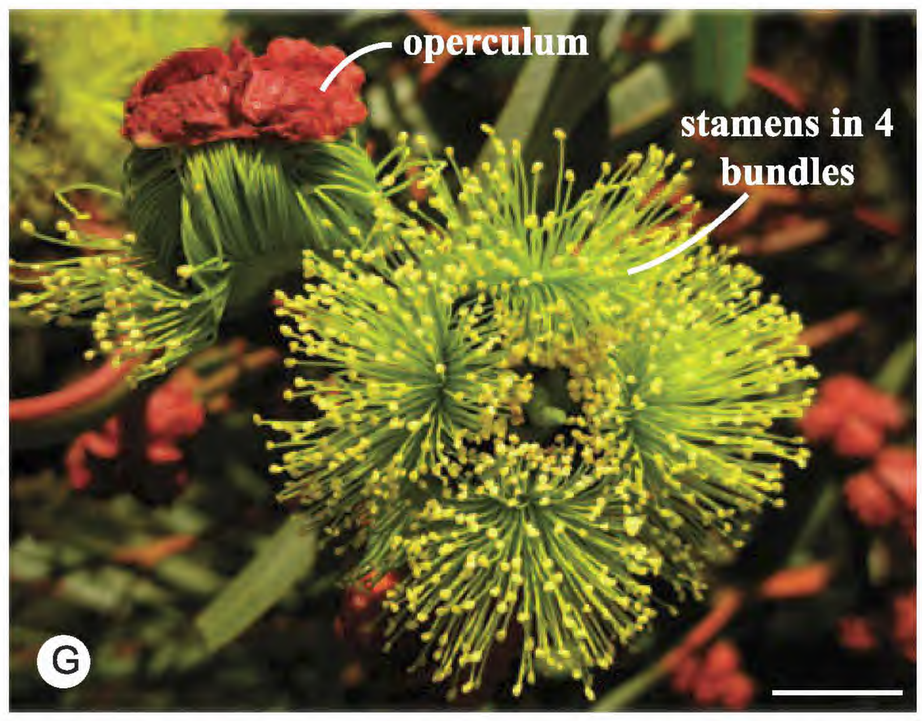












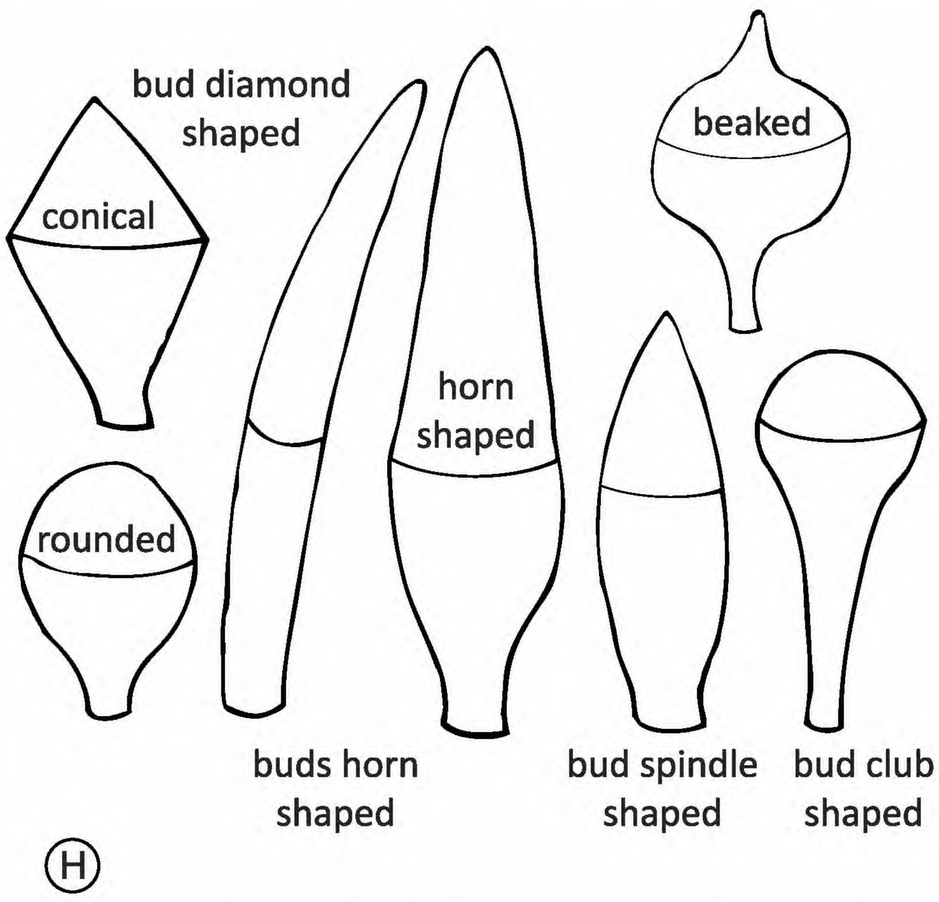


Figure 3. Inflorescence and flower characteristics in *Eucalyptus*. —A. Flower bud characteristics, showing the beaked operculum and stamens that are all bent inward under the operculum, taken from *E. incrassata* Labill. —B. Flower bud characteristics, illustrating the lack of an operculum scar, a rounded operculum, and stamens that are all fertile, taken from *E. diversicolor* F. Muell. —C. *Eucalyptus sideroxylon* A. Cunn. ex Woolls, showing umbels with a peduncle that is round in cross-section and flowers with outer stamens without anthers. —D, E. Stamen and floral bud characteristics. —F. *Eucalyptus eremophila* (Diels) Maiden, with the umbel showing a straplike peduncle and the flowers with horn-shaped opercula. —G. *Eucalyptus erythrocorys* F. Muell., with the flowers illustrating the bright red opercula and yellow stamens bundled in four groups within the flower. —H. Flower bud and operculum shapes. A–G scale bars = 1 cm.

18. Buds and fruits in clusters of 7 to 15, oval, sessile ..... *E. neglecta* (Omeo gum)
18′. Buds and fruits in clusters of 7, diamond-shaped, sessile or very shortly pedicellate ..... *E. conspicua* (Gippsland swamp-box)

Group 2, Ironbarks, Trees with Very Hard, Dark Bark

This group contains species called ironbarks in which the bark is impregnated with hardened kino (a dark gummy exudate), making the bark rough, thick, deeply furrowed, very hard (not easily pulled from tree), dark brown, gray, or black, and retained on trunk and limbs (Fig. 1F, *Eucalyptus sideroxylon* L. A. S. Johnson & K. D. Hill). These species primarily occur in eastern and northeastern Australia and are exemplified by *E. crebra* Labill. and *E. paniculata* Sm.

1. Leaves always opposite, glaucous on mature trees ..... *Eucalyptus melanophloia* (silver-leaved ironbark)
1′. Leaves mostly alternate, not glaucous on mature trees 2
2. Outer stamens without anthers 3
3. Adult leaves discolorous ..... *E. paniculata* (gray ironbark)
3′. Adult leaves concolorous 4
4. Buds and fruits in clusters of 7; leaves dull ..... *E. sideroxylon* (red ironbark)
4′. Buds and fruits in clusters of more than 7; leaves glossy ..... *E. sieberi* (silvertop ash)
2′. All stamens with anthers 5
5. Inflorescences unbranched umbels in leaf axils (not true ironbarks, but may be mistaken as such) ..... *E. bridgesiana* (apple box)
5′. Inflorescences compound (highly branched) clusters at branch tips 6
6. Operculum rounded; fruit valves enclosed ..... *E. crebra* (narrow-leaved ironbark)
6′. Operculum conical; fruit valves exserted 7
7. Operculum 1.5× hypanthium length; valves of mature fruit clearly exserted; fruit up to 1 cm wide ..... *E. fibrosa* (broad-leaved ironbark)
7′. Operculum equal to hypanthium; valves of mature fruit only slightly exserted or at rim level; fruit 0.5–0.7 cm wide ..... *E. siderophloia* (ironbark)

Group 3, Trees or Mallees with Discolorous Leaves

This group contains species with discolorous leaves (Fig. 2F, *Eucalyptus robusta*). The upper (adaxial) and lower (abaxial) surfaces of mature leaves are of different colors. The upper surface of the leaf is usually darker green than the lower surface. Examples of species with discolorous leaves are *Corymbia ficifolia* F. Muell. and *E. cladocalyx* F. Muell.

1. Adult leaves opposite; bark pink or orange, smooth to the ground; operculum absent ..... *Angophora costata* (apple gum)
1′. Adult leaves alternate; bark varying; operculum present 2
2. Mallee; sepals small, pointed, usually apparent on the buds and fruits ... *Eucalyptus curtisii* (Plunkett mallee)
2′. Tree; sepals fused into an operculum or sepals not apparent 3
3. Bark smooth and shedding completely, or bark rough on the trunk and shedding from the largest limbs and branches 4
4. Inflorescences compound, highly branched clusters at branch tips or in leaf axils 5
5. Bark multicolored, with orange and light green patches; fruit < 0.5 cm wide ..... *E. deglupta* (rainbow gum, Mindanao gum)
5′. Bark slaty green, dark green, or gray; fruit > 0.75 cm wide ..... *Corymbia torelliana* (blood-leaf gum, cadaghi)
4′. Inflorescences unbranched umbels in leaf axils 6
6. Valves of mature fruit clearly enclosed within fruit rim 7
7. Leaves highly shiny, leaf oil glands small, obscure; buds and fruits born on leafless sections of branchlets; operculum scar obvious; mature leaves often sickle-shaped; dried fruit with longitudinal ridges ..... *E. cladocalyx* (sugar gum)
7′. Leaves dull, leaf oil glands obvious; buds and fruits born in leaf axils; operculum scar obscure or absent; mature leaves lanceolate; dried fruit not ridged ... *E. diversicolor* (karri)
6′. Valves of mature fruit exserted beyond fruit rim or level with fruit rim 8
8. Valves of mature fruit at rim level or only slightly exserted 9
9. Bark shedding, mostly or completely smooth to the ground, occasionally with a short stocking of rough bark at the base ..... *E. deanei* (mountain blue gum)
9′. Bark retained on lower trunk, mostly rough and fibrous, smooth on upper branches ..... *E. urophylla* (Timor mountain gum)
8′. Valves of mature fruit strongly exserted 10
10. Bark gray, mottled, shed in patches, exposing orange, coppery new bark, usually smooth to the ground ..... *E. punctata* (gray gum)

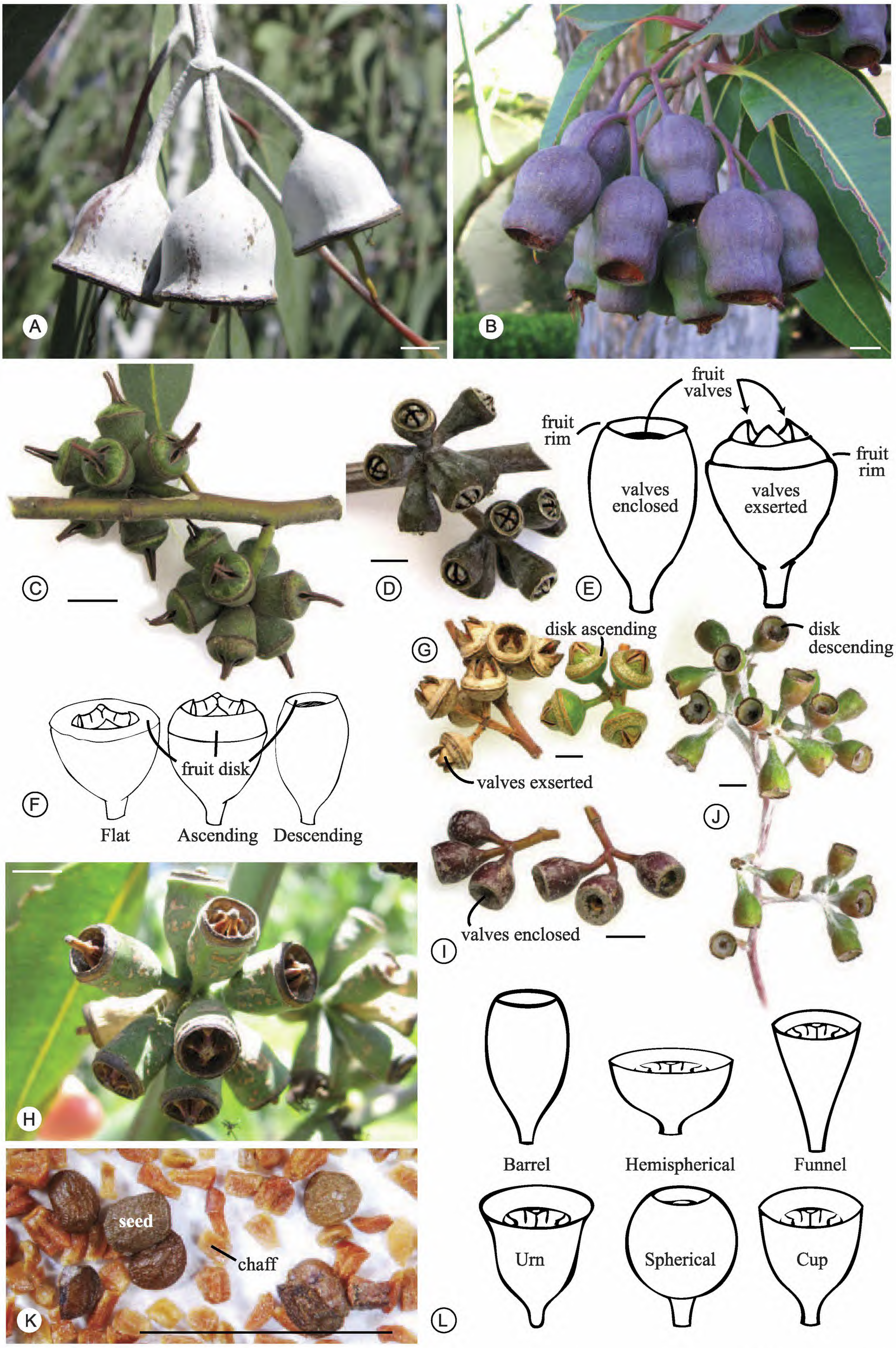


Figure 4. Fruit and seed diversity in eucalypts. —A. *Eucalyptus caesia* subsp. *magna* Brooker & Hopper, illustrating a 3-fruited cluster. —B. *Corymbia calophylla* (Lindl.) K. D. Hill & L. A. S. Johnson, with urn-shaped fruit. —C. *Eucalyptus cornuta* Labill., showing the exserted valve tips that are connected in mature fruit. —D. *Eucalyptus grandis* W. Hill, with mature fruits, each of which reveal four exserted and inward curved valves. —E. Fruit valve characteristics. —F. Fruit disk characteristics. —G. *Eucalyptus camaldulensis* Dehnh., with fruit having exserted valves and ascending disks. —H. *Eucalyptus robusta* Sm., with fruit valve tips connected in mature fruit, these valves persisting even after seeds are shed. —I. *Eucalyptus leucoxylon*

10′. Bark smooth and cream-colored, or pale gray, or white, sometimes fibrous and flaky at the base (to ca. 2 m above ground) or rough for most of the trunk and smooth on the branches 11
11. Valves of mature fruit 4 or 5, curved inward; buds often glaucous ..... *E. grandis* (rose gum)
11′. Valves of mature fruit usually 4, erect; buds not glaucous ..... *E. saligna* (Sydney blue gum)
3′. Bark rough, furrowed, retained on trunk and large limbs 12
12. Inflorescences as highly branched clusters at branch tips or in leaf axils 13
13. Valves of mature fruit level with fruit rim or exserted beyond fruit rim 14
14. Inflorescences compound, in leaf axils; all stamens with anthers; stamens not clustered ..... *E. cloeziana* (gympie messmate)
14′. Inflorescences at branch tips, outer stamens without anthers; stamens in 4 clusters ..... *E. microcorys* (tallowwood)
13′. Valves of mature fruit deeply enclosed 15
15. Fruit prominently ridged; buds scaly ..... *C. ptychocarpa* (swamp bloodwood)
15′. Fruit smooth; buds not scaly 16
16. Fruit < 1.5 cm wide ..... *C. gummifera* (red bloodwood)
16′. Fruit > 2 cm wide 17
17. Flowers pale orange to deep pink and red; seeds with a wing; leaf oil glands lacking or very sparse ..... *C. ficifolia* (red-flowering gum)
17′. Flowers white; seeds wingless; leaf oil glands numerous ... *C. calophylla* (marri)
12′. Inflorescences as unbranched umbels in leaf axils 18
18. Valves of the mature fruit fused across the fruit opening; fruit cylindrical to barrel-shaped ..... *E. robusta* (swamp mahogany)
18′. Valves of mature fruit free, not connected at the tips; fruit variously shaped 19
19. Valves of mature fruit clearly exserted beyond fruit rim 20
20. Fruit > 1.4 cm wide; fruit disk flat ..... *E. pellita* (large-fruited red mahogany)
20′. Fruit 1 cm or less wide; fruit disk ascending ..... *E. resinifera* (red mahogany)
19′. Valves of mature fruit enclosed, level with fruit rim, or slightly exserted 21
21. Buds and fruits glaucous; flowers bright orange ..... *E. miniata* (Darwin woollybutt)
21′. Buds and fruits green or brown; flowers white 22
22. Peduncles broad, flattened; buds and fruits sessile or nearly so; operculum scar present ..... *E. botryoides* (southern mahogany)
22′. Peduncles slender, round in cross-section; buds and fruits pedicellate; operculum scar absent 23
23. Leaves only slightly lighter on the underside 24
24. Leaves thin; operculum conical to beaked ..... *E. eugenioides* (thin-leaved stringybark)
24′. Leaves thicker, leathery; operculum rounded ..... *E. muelleriana* (yellow stringybark)
23′. Leaves distinctly lighter on the underside, leathery 25
25. Fruit > 1 cm wide; outer stamens erect under operculum when in bud ..... *E. marginata* (jarrah)
25′. Fruit 0.5–1 cm wide; outer stamens bent under operculum when in bud ..... *E. acmenoides* (white mahogany)

Group 4, Trees or Mallees with Compound, Highly Branched Inflorescences

This group contains species in which the flowers are formed in compound, panicle-like, highly branched clusters at branch tips (e.g., *Eucalyptus polyanthemos* Schauer) or in leaf axils (e.g., *Corymbia citriodora* (Hook.) K. D. Hill & L. A. S. Johnson) (cf. diagram, Fig. 2J).

1. Bark shedding, smooth to the ground 2
2. Outer stamens without anthers; inflorescences at branch tips (terminal) ..... *Eucalyptus polyanthemos* (red box, silver dollar gum)
2′. All stamens with anthers; inflorescences in leaf axils 3
3. Leaves lemon-scented when crushed ..... *Corymbia citriodora* (lemon-scented gum)
3′. Leaves with medicinal or spicy scent when crushed (but not like lemon) 4

←

F. Muell., with cup-shaped fruit that have enclosed valves, and fruit in clusters of three. —J. *Eucalyptus polyanthemos* Schauer, with fruit that have descending disks. —K. *Eucalyptus lansdowneana* F. Muell. & J. E. Br., seeds and chaff. —L. Diversity of fruit shapes. A–L scale bars = 1 cm.

4. Trunk uniformly smooth, not mottled, powdery to the touch; fruit thin-walled ..... *C. aparrerinja* (ghost gum)
4′. Trunk mottled, not powdery; fruit thick-walled ..... *C. maculata* (spotted gum)
1′. Bark rough, furrowed, retained on trunk and largest limbs (small branches may be smooth) 5
5. Mallee or multistemmed shrub; operculum scar absent 6
6. Flowers red to mauve to pink ..... *E. lansdowneana* (red-flowered mallee box)
6′. Flowers white, pink, or purple ..... *E. albopurpurea* (purple-flowered mallee)
5′. Tree; operculum scar present or absent 7
7. Bark yellowish or tan, flaky; leaves sickle-shaped; fruit barrel-shaped or urn-shaped; valves enclosed ..... *C. eximia* (yellow bloodwood)
7′. Bark gray, short-fibered, hard (box-type); most leaves lanceolate or ovate to elliptical; fruit variously shaped; valves enclosed or exserted 8
8. Valves of mature fruit clearly exserted beyond fruit rim ..... *E. coolabah* (coolibah)
8′. Valves of mature fruit enclosed or level with fruit 9
9. Operculum scar absent 10
10. Buds and fruits glaucous ..... *E. albens* (white box)
10′. Buds and fruits green or brown (not waxy) 11
11. Outer stamens without anthers; buds curved ..... *E. ochrophloia* (napunyah)
11′. All stamens with anthers; buds straight ..... *E. microcarpa* (inland box)
9′. Operculum scar present 12
12. Outer stamens without anthers; stamens shed together in a ring 13
13. Mature leaves glossy green ..... *E. baueriana* (round-leaved box)
13′. Mature leaves dull, gray-green, bluish green, or glaucous ..... *E. polyanthemos* (red box, silver dollar gum)
12′. All stamens with anthers; stamens shed individually 14
14. Bark of small branches rough 15
15. Leaves ovate to elliptical ..... *E. populnea* (Bimbil box)
15′. Leaves lanceolate ..... *E. largiflorens* (black box)
14′. Bark of small branches smooth, rough bark extending only to base of larger branches 16
16. Valves of mature fruit at rim level and sometimes slightly exserted; leaf oil glands obvious; intramarginal vein present ..... *E. microtheca* (tropical coolibah)
16′. Valves of mature fruit enclosed; leaf oil glands obscure or absent; intramarginal vein obscure or absent ..... *E. intertexta* (gum coolibah)

Group 5, Trees or Mallees with Buds and Fruits Solitary or in Clusters of Three in Leaf Axils

This group contains species in which the flowers are formed in clusters of three on a single stalk in the leaf axils (e.g., *Eucalyptus viminalis* Labill. and *E. cosmophylla* F. Muell.) or are formed solitarily in leaf axils (e.g., *E. globulus* Labill.) (cf. diagram, Fig. 2K).

1. Buds and fruits solitary 2
2. Buds and fruits glaucous; large tree ..... *Eucalyptus globulus* (blue gum, Tasmanian blue gum)
2′. Buds and fruits green, yellow, red, or brown (not waxy); small tree, mallee, or shrub 3
3. Buds round in cross-section, pear-shaped with many ribs ..... *E. stoatei* (scarlet pear gum)
3′. Buds square in cross-section, with 4 wings 4
4. Buds and fruits sessile, stiffly downturned; leaves thick; fruit > 2.5 cm wide ..... *E. tetraptera* (square-fruited mallee)
4′. Buds and fruits pedicellate, pendulous; leaves thin; fruit < 2.5 cm wide 5
5. Operculum slender and beaked ..... *E. dolichorhyncha* (fuchsia gum)
5′. Operculum flat and disklike ..... *E. forrestiana* (fuchsia gum)
1′. Buds and fruits in clusters of 3 6
6. Mallees or multistemmed shrubs 7
7. Operculum bright red; stamens in 4 clusters; adult leaves opposite or nearly so ..... *E. erythrocorys* (redcap gum, Illyarrie)
7′. Operculum red, brown, green, or glaucous; stamens not clustered; adult leaves alternate 8
8. Operculum smooth 9
9. Buds and fruits glaucous ..... *E. caesia* subsp. *magna* (silver princess)
9′. Buds and fruits green or brown (not waxy) 10
10. Valves of mature fruit strongly exserted; bark rough ..... *E. morrisii* (gray mallee)
10′. Valves of mature fruit only slightly exserted or level with fruit rim; bark smooth 11
11. Leaves < 4 cm long ..... *E. vernicosa* (varnished gum)
11′. Leaves > 6 cm long 12
12. Operculum rounded and flattened; fruit bell-shaped ..... *E. preissiana* (bell-fruited mallee)

12′. Operculum beaked or conical; fruit cup-shaped, cylindrical, or funnel-shaped 13
13. Flowers red to pale yellow; fruit funnel-shaped ..... *E. erythronema* (red-flowered mallee)
13′. Flowers white; fruit cup-shaped or cylindrical ... *E. cosmophylla* (cup gum)
8′. Operculum distinctly ribbed or warty 14
14. Operculum warty, scar absent 15
15. Valves enclosed; bark smooth ..... *E. coccifera* (Tasmanian snow gum)
15′. Valves exserted; bark rough ..... *E. serraensis* (Grampians stringybark)
14′. Operculum ribbed, scar present 16
16. Buds and fruits sessile or nearly so 17
17. Leaves glossy green; fruit cylindrical, < 2.5 cm wide ..... *E. angulosa* (ridge-fruited mallee)
17′. Leaves dull, green to blue-green; fruit disk-shaped, > 3 cm wide ..... *E. youngiana* (large-fruited mallee)
16′. Buds and fruits clearly pedicellate (pedicels as long as or longer than hypanthium) ... 18
18. Peduncles stout; fruit with 4 or 5 prominent ridges; bark usually smooth to the ground ..... *E. pyriformis* (Dowerin rose)
18′. Peduncles slender; fruit with > 5 prominent ridges; bark usually rough at the base ..... *E. kingsmillii* (Kingsmill's mallee)
6′. Trees 19
19. Bark rough, furrowed, retained on trunk and limbs ..... *E. longifolia* (woollybutt)
19′. Bark smooth, shedding (sometimes with imperfectly shed rough bark on the basal area of trunk) 20
20. Outer stamens without anthers; flowers red, pink, yellow, orange or white ..... *E. leucoxylon* (white ironbark)
20′. All stamens with anthers; flowers white 21
21. Buds and fruits distinctly square in cross-section ..... *E. steedmanii* (Steedman's mallet)
21′. Buds and fruits round in cross-section or only slightly angled 22
22. Operculum warty and with a central knob; peduncle stout or absent 23
23. Peduncles absent ..... *E. bicostata* (Victorian blue gum)
23′. Peduncles present ..... *E. pseudoglobulus* (Victorian eurabbie)
22′. Operculum smooth or warty, but without a central knob (a beak may be present); peduncle slender 24
24. Valves of mature fruit exserted; fruit disk raised 25
25. Buds and fruits glaucous ..... *E. rubida* (blackbutt candlebark)
25′. Buds and fruits green or brown (not waxy) 26
26. Juvenile leaves lanceolate, glossy, green ..... *E. viminalis* (manna gum, ribbon gum)
26′. Juvenile leaves ovate to elliptical, dull, blue-green ..... *E. dalrympleana* (broad-leaved ribbon gum)
24′. Valves of mature fruit enclosed or level with fruit rim; fruit disk descending or flat .. 27
27. Buds and fruits sessile or pedicels 0.2 cm or less 28
28. Juvenile leaves fused into a single disk; fruit 0.5–0.8 cm wide ..... *E. perriniana* (spinning gum)
28′. Juvenile leaves not fused; fruit 0.8–1.2 cm wide ..... *E. glaucescens* (Tingiringi gum)
27′. Buds and fruits pedicellate 29
29. Peduncles as long as or longer than buds, often downturned; fruit urn-shaped ..... *E. urnigera* (urn gum)
29′. Peduncles shorter than buds, erect; fruit hemispherical, barrel- or slightly urn-shaped 30
30. Leaves glossy with a hooked tip; operculum scar absent; buds warty ..... *E. coccifera* (Tasmanian snow gum)
30′. Leaves dull, gray-green or bluish green, with a pointed tip; operculum scar present; buds smooth ..... *E. gunnii* (cider gum)

Group 6, Trees without an Operculum Scar but with Acutely Angled or Parallel Leaf Veins, and Buds and Fruits in Clusters of More than Seven

This group contains species in which the mature flower buds do not have an operculum scar. Such buds have a single operculum with no circumferential scar on the bud surface caused by the shedding of the outer operculum, as happens in many other eucalypts (cf. Fig. 2P). In this group the buds and fruits are usually in clusters of 11 or more, the disk of the fruit is reddish brown, shiny, and level with the fruit rim (cf. diagrams in Fig. 4E, F). Species in this group also make leaves in which the side leaf veins are few, acutely angled, or parallel (Fig. 2H, *Eucalyptus stellulata* Sieber ex DC.). Exemplar species in the group are *E. pauciflora* Sieber ex Spreng. and *E.*

amygdalina Labill. Taxa in group 6 include the widely grown and naturalized members of *Eucalyptus* subg. *Eucalyptus*, but this is only a partial treatment of this subgenus, which contains approximately 120 taxa.

1. Buds and fruits in clusters of 7 2
   2. Buds green, pedicellate; outer stamens without anthers ..... *Eucalyptus melliodora* (honey box)
   2′. Buds glaucous, sessile; all stamens with anthers ..... *E. albens* (white box)
1′. Buds and fruits in clusters of more than 7 3
   3. Inflorescences usually paired umbels in leaf axils 4
      4. Bark rough, fibrous, retained on both the trunk and limbs ..... *E. fastigata* (brown barrel)
      4′. Bark rough on the lower trunk only; large limbs smooth ..... *E. regnans* (mountain ash)
   3′. Inflorescences always single umbels in leaf axils 5
      5. Leaves with side veins nearly parallel or prominently 3-veined 6
         6. Leaf side veins nearly parallel; buds club-shaped, rounded, sometimes warty ..... *E. pauciflora* (snow gum)
         6′. Leaves prominently 3-veined; buds spindle-shaped, pointed, smooth ..... *E. stellulata* (black sally)
      5′. Leaves with side veins angling toward leaf margin, not parallel-veined or 3-veined 7
         7. Bark rough, fibrous, retained on the entire trunk and large limbs, extending to the small branches ... 8
            8. Outer stamens without anthers ..... *E. sieberi* (silvertop ash)
            8′. All stamens with anthers 9
               9. Most leaves 0.4–1 cm wide ..... *E. amygdalina* (black peppermint)
               9′. Most leaves > 1 cm wide 10
                  10. Adult leaf bases clearly oblique; juvenile leaves pendulous, usually > 6 cm wide, glossy green, petiolate ..... *E. obliqua* (messmate stringybark)
                  10′. Adult leaf bases tapering evenly or almost evenly to the petiole, or occasionally oblique; juvenile leaves upright, usually < 5 cm wide, glaucous or green, sessile or petiolate 11
                     11. Juvenile leaves opposite, sessile; adult leaves always concolorous 12
                        12. Juvenile leaves ovate, gray-green to glaucous ... *E. dives* (blue peppermint)
                        12′. Juvenile leaves narrowly lanceolate or linear, green ..... *E. radiata* (narrow-leaved peppermint)
                     11′. Juvenile leaves alternate, petiolate; adult leaves slightly discolorous or concolorous 13
                        13. Leaves thin; operculum conical to beaked ..... *E. eugenioides* (thin-leaved stringybark)
                        13′. Leaves thicker, leathery; operculum rounded ..... *E. muelleriana* (yellow stringybark)
         7′. Bark smooth, shedding completely, or rough on lower trunk only, with smooth upper trunk and/or large limbs 14
            14. Bark rough on lower trunk only with smooth upper trunk or large limbs 15
               15. Fruit sessile or pedicel < 0.4 cm long ..... *E. olsenii* (Olsen's gum, Woila gum)
               15′. Fruit clearly pedicellate 16
                  16. Peduncles flattened ..... *E. pilularis* (blackbutt)
                  16′. Peduncles round in cross-section or slightly angular 17
                     17. Bark finely fibrous, gray or brown; fruit barrel-shaped; buds often glaucous ..... *E. delegatensis* (alpine ash)
                     17′. Bark furrowed, compact, brown-black; fruit cup-shaped; buds green ..... *E. elata* (river peppermint)
            14′. Bark completely smooth, shedding to the ground 18
               18. Young branches, buds, and fruits warty and glaucous ... *E. coccifera* (Tasmanian snow gum)
               18′. Young branches, buds, and fruits smooth, green or brown 19
                  19. Leaves linear or narrowly lanceolate, smelling of peppermint when crushed ... *E. pulchella* (white peppermint)
                  19′. Leaves lanceolate, without peppermint smell 20
                     20. Fruit 0.9 × 0.9 cm ..... *E. haemastoma* (scribbly gum)
                     20′. Fruit up to 0.6 × 0.7 cm ..... *E. racemosa* (scribbly gum)

Group 7, Trees, Mallees, and Shrubs with Flattened Straplike Peduncles

This group contains species in which the peduncle (the common stalk of the cluster of flowers) is broad, flattened, and straplike (Fig. 3F, *Eucalyptus eremophila* (Diels) Maiden) as opposed to being round in cross-section (Fig. 2C, *E. torquata*). Exemplar species in group 7 are *E. gomphocephala* A. Cunn. ex DC. and *E. utilis* Brooker & Hopper.

1. Valves of mature fruit clearly exserted beyond fruit rim 2
   2. Buds glaucous; operculum warty and with a central knob ..... *Eucalyptus maidenii* (Maiden's gum)

2′. Buds green, yellow, or brown; operculum without a central knob 3
3. Valve tips connected in mature fruit (after seed is shed) 4
4. Branchlet pith glandular ..... *E. cornuta* (yate)
4′. Branchlet pith without oil glands 5
5. Buds and fruits fused at the base 6
6. Apical bud at shoot tip 1–2.2 cm long, feeling triangular when rolled between finger and thumb; peduncle thick, 2–4 cm long; lacking a lignotuber ..... *E. conferruminata* (Bald Island marlock)
6′. Apical bud at shoot tip < 1 cm long, not triangular; peduncle thin; forming a lignotuber ..... *E. lehmannii* (bushy yate)
5′. Buds and fruits not fused at the base 7
7. Operculum smooth or only slightly warty; forming a lignotuber ... *E. talyuberlup* (pretty yate)
7′. Operculum very warty; lacking a lignotuber ..... *E. megacornuta* (warted yate)
3′. Valve tips free in mature fruit 8
8. Leaf veins obscured by numerous oil glands; fruit valves prominent, stout ..... *E. annulata* (open-fruit mallee)
8′. Leaf veins obvious; fruit valves slender 9
9. Bark rough at the base and smooth above; operculum 1.5 to 2.5× longer than hypanthium; forming a lignotuber ..... *E. occidentalis* (flat-topped yate)
9′. Bark smooth to the ground, sometimes with partly detached flakes; operculum equal in length to the hypanthium; lacking a lignotuber ..... *E. astringens* (brown mallet)
1′. Valves of mature fruit enclosed, level with fruit rim, or slightly exserted 10
10. Branchlet pith without oil glands 11
11. Operculum horn-shaped, 2 to 3× longer than hypanthium ..... *E. gardneri* (blue mallet)
11′. Operculum conical to beaked, equal in length to hypanthium ..... *E. cypellocarpa* (monkey gum)
10′. Branchlet pith glandular 12
12. Peduncles glaucous ..... *E. stricklandii* (Strickland's gum)
12′. Peduncles green, yellow, or brown (not waxy) 13
13. Bark rough, furrowed, retained on trunk and limbs; buds shaped like mushrooms ..... *E. gomphocephala* (tuart)
13′. Bark smooth, shedding (sometimes with imperfectly shed rough bark on the basal area of trunk); buds variously shaped 14
14. Buds and fruits usually in clusters of more than 7 15
15. Operculum conical or rounded ..... *E. accedens* (powder bark wandoo)
15′. Operculum horn-shaped 16
16. Leaves very glossy, green; flowers yellow ..... *E. macrandra* (river yate)
16′. Leaves dull, slightly blue-green; flowers white ..... *E. wandoo* (wandoo)
14′. Buds and fruits in clusters of 7 17
17. Some or all stamens inflexed in bud (bent downward under operculum); operculum rounded, conical or beaked 18
18. Operculum narrower than the rest of the bud; flowers red, yellow, or chartreuse ..... *E. cernua* (red-flowered moort)
18′. Operculum same width as the rest of the bud; flowers white ..... *E. incrassata* (ridge-fruited mallee)
17′. All stamens erect when in bud (not bent under operculum); operculum conical or horn-shaped 19
19. Buds smooth, not ridged ..... *E. eremophila* (sand mallet)
19′. Buds ridged or winged 20
20. Leaves lanceolate (usually > 5× longer than wide) ..... *E. utilis* (coastal moort)
20′. Leaves orbicular or ovate (usually < 3× longer than wide) 21
21. Operculum 1.5 to 3× longer than the rest of the bud; valves 4; flowers yellow ..... *E. platypus* (moort)
21′. Operculum same length as the rest of the bud; valves 5 or 6; flowers red ..... *E. nutans* (red-flowered moort)

Group 8, Trees and Mallees Having Fruit with Enclosed Valves or Valves Level with the Fruit Rim

This group contains species in which the mature fruit form valves (the distal end of the capsule that dehisces to allow for seed dispersal) are enclosed and do not emerge from inside the hypanthium (or fruit rim), or that extend to the level of the fruit rim, but not beyond it. Examples of species with valves of mature dehiscent fruit that are either sunken below (proximal to) the fruit rim (e.g., *Eucalyptus torquata* Luehm.) or level with fruit rim (e.g., *E. spathulata* Hook.) (cf. Fig. 4E, G, *E. camaldulensis* Dehnh., 4I, *E. leuoxylon* F. Muell.).

1. Mallees or multistemmed shrubs 2
2. Buds and fruits square in cross-section 3

3. Outer stamens without anthers, flowers white or pink ..... *Eucalyptus calycogona* (square-fruited mallee)
3′. All stamens with anthers, flowers yellow ..... *E. roycei* (Shark Bay mallee)
2′. Buds and fruits round in cross-section 4
4. Buds and fruits glaucous ..... *E. caesia* subsp. *caesia* (caesia)
4′. Buds and fruits not covered with wax 5
5. Leaves held upright on the stem (ascending) ... *E. cneorifolia* (Kangaroo Island narrow-leaved mallee)
5′. Leaves hanging vertically or perpendicular to the stem (spreading) 6
6. Leaves usually with lenticels (indentations) along the edges; buds usually ribbed; operculum beaked ..... *E. incrassata* (ridge-fruited mallee)
6′. Leaves lacking indentations on the distal margins; buds ribbed or not; operculum variously shaped 7
7. Branchlet pith glandular 8
8. Bark rough to the smallest stems 9
9. Peduncles slender, upright; buds pedicellate; flowers white . . . . *E. loxophleba* (York gum)
9′. Peduncles stout, prominently downturned; buds sessile; flowers yellow . . . . *E. grossa* (coarse-leaved mallee)
8′. Bark smooth, or rough only on the lower portion of the trunk 10
10. Flowers red or yellow; fruit funnel-shaped ... *E. erythronema* (red-flowered mallee)
10′. Flowers white; fruit cylindrical to barrel-shaped 11
11. Leaves glossy, linear to narrowly lanceolate, < 1 cm wide . . . . *E. cylindrocarpa* (woodline mallee)
11′. Leaves dull, lanceolate, > 1.5 cm wide ..... *E. dumosa* (white mallee)
7′. Branchlet pith without oil glands 12
12. Bark smooth 13
13. Buds and fruits sessile or shortly pedicellate (< 0.2 cm) . . . . *E. kitsoniana* (Gippsland mallee)
13′. Buds and fruits pedicellate ..... *E. flocktoniae* (merrit)
12′. Bark rough 14
14. Leaves with conspicuous black oil dots; operculum scar present . . . . *E. gracilis* (white mallee)
14′. Leaves lacking black dots; operculum scar absent 15
15. Leaves linear or narrowly lanceolate, green; buds green . . . . *E. viridis* (green mallee)
15′. Leaves lanceolate, bluish gray or bluish green; buds glaucous . . . . *E. polybractea* (blue-leaved mallee)
1′. Trees 16
16. Buds and fruits sessile or shortly pedicellate (< 0.2 cm) 17
17. Crown of adult trees contain sessile juvenile leaves ..... *E. parvula* (small-leaved gum)
17′. Crown of adult trees with petiolate adult leaves only 18
18. Branchlet pith glandular ..... *E. dundasii* (Dundas blackbutt)
18′. Branchlet pith without oil glands 19
19. Bark rough to small branches ..... *E. goniocalyx* (long-leaved box)
19′. Bark mostly smooth 20
20. Inflorescence often subtended by a prominent bract; bark coppery in color; operculum rounded ..... *E. kitsoniana* (Gippsland mallee)
20′. Inflorescence not subtended by a bract; bark pale gray or cream-colored; operculum conical ..... *E. nitens* (silvertop)
16′. Buds and fruits pedicellate 21
21. Bark smooth, shedding completely to the ground 22
22. Flowers lemon yellow; bark white or gray; leaves lanceolate, dull; buds glaucous . . . . *E. woodwardii* (lemon-flowered gum)
22′. Flowers white; bark coppery or pinkish gray; leaves linear or narrowly lanceolate, glossy; buds green 23
23. All stamens erect in bud (not bent under operculum); operculum horn-shaped; leaves linear, < 0.5 cm wide ..... *E. spathulata* (swamp mallet)
23′. Stamens inflexed in bud (bent downward under operculum); operculum rounded, beaked or conical; leaves lanceolate to narrowly lanceolate, > 0.5 cm wide 24
24. Buds conspicuously ribbed ..... *E. pterocarpa* (Norseman gum)
24′. Buds smooth ..... *E. cylindrocarpa* (woodline mallee)
21′. Bark rough, retained on lower trunk, bark on limbs rough or smooth 25
25. Outer stamens without anthers; branchlet pith without oil glands 26
26. Leaves with conspicuous black oil dots; operculum scar present; operculum rounded or flattened ..... *E. gracilis* (white mallee)
26′. Leaves lacking black dots; operculum scar absent; operculum beaked or conical . . . . *E. melliodora* (honey box)
25′. All stamens with anthers; branchlet pith glandular 27

27. Bark rough to the smallest branches ..... *E. loxophleba* (York gum)
27′. Bark rough at the base, smooth and shedding on small branches 28
28. Flowers pink; leaves dull, bluish green; branchlets green, yellow or red ..... *E. torquata* (coral gum)
28′. Flowers white; leaves green; branchlets often glaucous ..... *E. lesouefii* (Goldfields' blackbutt)

Group 9, Trees and Mallees Having Fruit with Valves Clearly Exserted Beyond the Rim of the Fruit

This group contains species in which the valves of the mature fruit are clearly exserted beyond (distal to) the rim of the fruit or hypanthium (e.g., *Eucalyptus camaldulensis* Dehnh. and *E. mannifera* Mudie) (Fig. 4C, E, G).

1. Branchlets and buds glaucous 2
2. Leaves ovate to elliptical ..... *Eucalyptus orbifolia* (round-leaved mallee)
2′. Leaves lanceolate 3
3. Operculum longer than hypanthium ..... *E. blakelyi* (Blakely's red gum)
3′. Operculum equal in length to hypanthium ..... *E. dealbata* (hill red gum)
1′. Branchlets not covered with wax 4
4. Bark rough, furrowed, retained on most or all of the trunk, upper limbs either rough or smooth 5
5. Buds and fruits clearly sessile ..... *E. goniocalyx* (long-leaved box)
5′. Buds and fruits pedicellate, even if shortly so 6
6. Mallee or shrub 7
7. Leaves linear, < 0.5 cm wide ..... *E. formanii* (die hardy mallee)
7′. Leaves lanceolate, > 0.75 cm wide 8
8. Valves needlelike, fragile ..... *E. oleosa* (red morrell)
8′. Valves broad, 3-lobed ..... *E. mannensis* (Mann Range mallee)
6′. Tree 9
9. Bark shedding in long ribbons from upper limbs and sometimes upper part of the trunk ... 10
10. Bark loosely fibrous and fissured; fruit disk not prominent, flat or slightly raised ... . *E. macarthurii* (Paddy's River box)
10′. Bark rough and compact; fruit disk prominent, clearly ascending ..... *E. smithii* (blackbutt peppermint)
9′. Bark not shedding in ribbons, rough to the smallest branches or smooth on the smallest branches 11
11. Juvenile leaves very glaucous, crenulate ..... *E. bridgesiana* (apple box)
11′. Juvenile leaves only slightly waxy, or green, not crenulate (entire) 12
12. Fruit sessile or nearly so (pedicels < 0.2 cm long) ..... *E. aggregata* (black gum)
12′. Fruit pedicellate 13
13. Disk of fruit steeply ascending ..... *E. brassiana* (Cape York red gum)
13′. Disk of fruit level or only slightly ascending 14
14. Bark fibrous, brown; leaves narrowly lanceolate; disk of fruit thin, slightly ascending ..... *E. nicholii* (narrow-leaved black peppermint)
14′. Bark rough, compact, gray; leaves lanceolate to broadly lanceolate to ovate; disk of fruit broad, level ..... *E. rudis* (flooded gum)
4′. Bark smooth, shedding (sometimes with imperfectly shed rough bark on basal area); upper limbs smooth ... 15
15. Branchlet pith glandular 16
16. Flowers yellow or chartreuse; fruit with a prominent flange around the rim; bark brownish or greenish ..... *E. dielsii* (cap-fruited mallet)
16′. Flowers white; fruit without a flange; bark tan or coppery ..... *E. salubris* (gimlet)
15′. Branchlet pith without oil glands 17
17. Bark coppery, salmon-pink, or orange, shiny; leaves glossy, dark green, linear or narrowly lanceolate; fruit valves thin, needlelike ..... *E. salmonophloia* (salmon gum)
17′. Bark white, gray, tan, mottled, dull; leaves green, dull bluish green, or olive-green, lanceolate; fruit valves prominent, triangular 18
18. Bark white, powdery to the touch 19
19. Leaves dull, bluish green ..... *E. mannifera* (brittle gum, red spotted gum)
19′. Leaves glossy green ..... *E. scoparia* (Wallangara white gum)
18′. Bark gray or tan, sometimes white, not powdery 20
20. Fruit funnel-shaped; leaves glossy, often lacking oil glands ..... *E. ovata* (black gum, swamp gum)
20′. Fruit cup-shaped or hemispherical; leaves dull, with translucent oil glands 21
21. Juvenile leaves opposite for more than 10 pairs ..... *E. dunnii* (Dunn's white gum)
21′. Juvenile leaves opposite for fewer than 5 pairs 22

22. Operculum hemispheric, with a distinct beak, equal in length to hypanthium; branches often drooping ..... *E. camaldulensis* (red gum, river red gum)
22′. Operculum horn-shaped or conical, not beaked, 2× longer than hypanthium; branches often steeply ascending ..... *E. tereticornis* (forest red gum)

Taxonomic Treatment

Following the nomenclatural citation for those eucalypt species treated, common names are given. Each taxon is vouchered by a specimen and herbarium of deposit. Preceding the scientific name are two numbers that represent the taxon's position in the key. The key's group number is given first, followed by the particular couplet number in parentheses for the species considered. Both native ranges and the regional locations of naturalized populations, if known, are included. Eucalypt species without documented naturalized populations are included that are either persistent from cultivation or that are in wide horticultural use (e.g., plantations, honey production, shade, windbreaks, ornamentals).

I. Angophora Cav., Icon. 4: 21. 1797. *Eucalyptus* subg. *Angophora* (Cav.) Brooker, Austral. Syst. Bot. 13: 85. 2000. TYPE: *Angophora cordifolia* Cav.

Trees; bark rough or smooth. Leaves opposite, discolorous. Inflorescences compound, at branch tips. Flowers with the sepals persistent on woody fruit and the petals free within the inner floral whorl. Approximately 15 taxa, one of which is naturalized.

3 (1). Angophora costata (Gaertn.) Hochr. ex Britten, J. Bot. 54: 62. 1916. Basionym: *Metrosideros costata* Gaertn., Fruct. Sem. Pl. 1: 171. 1788.

Common name: apple gum.

Voucher: U.S.A. California, *Yost & Ritter 235* (OBI).

Native to: New South Wales, Queensland. Naturalized: California.

Trees; bark smooth, pink to orange. Leaves opposite, discolorous, lanceolate, petioled. Inflorescences compound, at branch tips. Flower buds with 5 small persistent sepal teeth; petals and stamens white. Fruits barrel-shaped to cylindrical, ribbed; valves enclosed.

II. Corymbia K. D. Hill & L. A. S. Johnson, Telopea 6: 214. 1995. *Eucalyptus* subg. *Corymbia* (K. D. Hill & L. A. S. Johnson) Brooker, Austral. Syst. Bot. 13: 85. 2000. TYPE: *Corymbia gummifera* (Gaertn.) K. D. Hill & L. A. S. Johnson [≡ *Metrosideros gummifera* Gaertn.].

Trees; bark rough or smooth. Leaves alternate, discolorous or concolorous, usually lanceolate, entire. Inflorescences compound, at branch tips or in leaf axils. Outer operculum held to just before flowering; operculum scar usually absent. Approximately 100 taxa, with nine species considered here.

4 (4). Corymbia aparrerinja K. D. Hill & L. A. S. Johnson, Telopea 6: 453. 1995.

Common name: ghost gum.

Voucher: Australia, Gosse Range, SW Macdonnell Ranges, May 1925, *H. Basedow s.n.* (type, NSW-10075, not seen).

Native to: North West Australia, North Australia, Queensland.

Trees; bark uniformly smooth, powdery, not mottled, white. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences compound, in leaf axils. Flowers white, all stamens with anthers. Fruits cup-shaped, thin-walled.

3 (17′). Corymbia calophylla Lindl., Telopea 6: 240. 1995. Basionym: *Eucalyptus calophylla* Lindl., Edwards' Bot. Reg. 27(157): 72. 1841.

Common name: marri.

Voucher: U.S.A. California, *Ritter 93* (OBI).

Native to: South West Austrailia. Naturalized: Hawaii, New Zealand.

Trees; bark rough, flaky, brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences compound, at branch tips; operculum scar absent. Flowers white. Fruits urn-shaped, thick, woody, > 2 cm wide; valves enclosed; seeds wingless.

4 (3). Corymbia citriodora (Hook.) K. D. Hill & L. A. S. Johnson, Telopea 6: 388. 1995. Basionym: *Eucalyptus citriodora* Hook., J. Exped. Trop. Australia 235. 1848.

Common name: lemon-scented gum.

Voucher: U.S.A. California, *Eastwood s.n.* (CAS-45201).

Native to: Queensland. Naturalized: California, Hawaii, India, South Africa, South West Australia, Victoria, Zimbabwe.

Trees; bark smooth, white, cream, to pink. Leaves alternate, concolorous, narrowly lanceolate, lemon-scented. Inflorescences compound, in leaf axils. Flowers white. Fruits urn-shaped or barrel-shaped; valves enclosed.

4 (7). Corymbia eximia (Schauer) K. D. Hill & L. A. S. Johnson, Telopea 6: 383. 1995. Basionym: *Eucalyptus eximia* Schauer in Walp., Repert. Bot. Syst. 2(5): 925–926. 1843.

Common name: yellow bloodwood.

Voucher: U.S.A. California, *Yost & Ritter 273* (OBI).

Native to: New South Wales.

Trees; bark rough, yellowish or tan, flaky. Leaves alternate, concolorous, sickle-shaped, dull, bluish green. Fruits barrel-shaped or urn-shaped; valves enclosed.

3 (17). Corymbia ficifolia (F. Muell.) K. D. Hill & L. A. S. Johnson, Telopea 6: 245. 1995. Basionym: *Eucalyptus ficifolia* F. Muell., Fragm. 2(13): 85. 1860.

Common name: red-flowering gum.

Voucher: U.S.A. California, *B. W. Thompson 515* (OBI).

Native to: South West Australia. Naturalized: Hawaii, New Zealand, South Africa.

Trees; bark rough, flaky, brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences compound, at branch tips; operculum scar absent. Flowers red, orange, pink. Fruits urn-shaped, thick, woody, > 2 cm wide; valves enclosed; seed winged.

3 (16). Corymbia gummifera (Sol. ex Gaertn.) K. D. Hill & L. A. S. Johnson, Telopea 6: 233. 1995. Basionym: *Metrosideros gummifera* Gaertn., Fruct. Sem. Pl. 1: 170, tab. 34, fig. I.

Common name: red bloodwood.

Voucher: U.S.A. California, *Ritter 68* (OBI).

Native to: New South Wales, Southern Queensland.

Trees; bark rough, flaky, brown. Leaves alternate, discolorous, lanceolate. Inflorescences compound, at branch tips; operculum scar absent. Flowers white. Fruits urn-shaped, thick, woody, < 1.5 cm wide; valves enclosed.

4 (4′). Corymbia maculata (Hook.) K. D. Hill & L. A. S. Johnson, Telopea 6: 393. 1995. Basionym: *Eucalyptus maculata* Hook., Icon. Pl. 7, pl. 619. 1944.

Common name: spotted gum.

Voucher: U.S.A. California, *Ritter 123* (OBI).

Native to: New South Wales, Victoria. Naturalized: Hawaii, South Africa, South West Australia.

Trees; bark smooth, mottled cream, yellow, gray, pink, to green or brown, shed in plates. Leaves alternate, concolorous, broadly lanceolate. Inflorescences compound, in leaf axils. Flowers white. Fruits urn-shaped or barrel-shaped; valves enclosed.

3 (15). Corymbia ptychocarpa (F. Muell.) K. D. Hill & L. A. S. Johnson, Telopea 6: 250. 1995. Basionym: *Eucalyptus ptychocarpa* F. Muell., J. Proc. Linn. Soc., Bot. 3: 90. 1859.

Common name: swamp bloodwood.

Voucher: Australia, Northern Territory, Gulf of Carpentaria, 22 July 1856, *F. Mueller s.n.* (type, K, not seen).

Native to: North West Australia, North Australia, Northern Queensland.

Trees; bark rough, fibrous, flaky, brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences compound, at branch tips. Buds ribbed, scaly; operculum scar absent. Flowers white. Fruits barrel-shaped, ribbed, ridged; valves enclosed.

3 (5′). Corymbia torelliana (F. Muell.) K. D. Hill & L. A. S. Johnson, Telopea 6: 385. 1995. Basionym: *Eucalyptus torelliana* F. Muell., Fragm. (Mueller) 10(87): 106–107. 1877.

Common name: blood-leaf gum or cadaghi.

Voucher: U.S.A. California, *Yost & Ritter 314* (OBI).

Native to: Northern Queensland. Naturalized: China, Florida, Hawaii, Queensland.

Trees; bark smooth, slaty-green, dark green, or gray, older trees with a rough stocking of bark on the lower trunk. Leaves alternate, discolorous, broadly lanceolate, some leaves in crown covered by bristly glands. Inflorescences compound, at branch tips. Flowers white. Fruits urn-shaped, sessile or nearly so, > 0.75 cm wide; valves enclosed.

III. Eucalyptus L'Hér., Sert. Angl., 18. 1788 [Jan. 1789]. TYPE: *Eucalyptus obliqua* L'Hér.

Trees, mallees, or shrubs; lignotuber present or absent; bark rough or smooth. Leaves alternate or opposite, discolorous or concolorous, linear, lanceolate to orbicular. Inflorescences compound, at branch tips, or axillary unbranched umbels, or flowers solitary in leaf axils. Operculum scar present or absent. At anthesis, flowers usually white, also red, pink, or yellow in some species. Fruits woody, usually cup-, barrel-, bell-, or urn-shaped; valves exserted, enclosed, or at rim level. Approximately 700 taxa, with 163 species known from cultivation and considered herein.

7 (15). Eucalyptus accedens W. Fitzg., J. Western Australia Nat. Hist. Soc. 1: 21. 1904.

Common name: powder bark wandoo.

Voucher: Australia, near Pingelly, Nov. 1903, *W. V. Fitzgerald s.n.* (type, NSW, not seen).

Native to: South West Australia.

Trees; bark smooth; branchlet pith glandular. Leaves alternate, concolorous, lanceolate. Inflorescences axillary; peduncle broad, flattened, and straplike. Buds 7, 9, or 11 per umbel; operculum conical or rounded, operculum scar present. At anthesis, flowers white. Fruits barrel-shaped; valves at rim level or slightly exserted.

3 (25′). Eucalyptus acmenoides Schauer in Walp., Bot. Syst. 2(5): 924. 1843.

Common name: white mahogany.

Voucher: U.S.A. California, *C. T. White 9072* (UC).

Native to: New South Wales, Queensland.

Trees; bark rough, fibrous. Leaves alternate, discolorous, lanceolate. Inflorescences axillary umbels; buds 11 to 15 per umbel; operculum conical to beaked, operculum scar absent. At anthesis, flowers white; all stamens with anthers; outer stamens inflexed in bud (bent downward under operculum). Fruits 0.5–1 cm wide, hemispherical to cup-shaped; valves at rim level or enclosed, tips free.

9 (12). Eucalyptus aggregata H. Deane & Maiden, Proc. Linn. Soc. New South Wales 24: 614. 1900.

Common name: black gum.

Voucher: U.S.A. California, *Yost & Ritter 205* (OBI).

Native to: New South Wales, Victoria.

Trees; bark rough, gray-brown, fibrous to the smallest branches. Leaves alternate, concolorous, lanceolate. Inflorescences as axillary umbels; buds 7 per umbel; operculum scar present. At anthesis, flowers white. Fruits nearly sessile (pedicels < 0.2 cm long); valves exserted.

4 (10) and 6 (2′). Eucalyptus albens Benth., Fl. Austral. 3: 219. 1867.

Common name: white box.

Voucher: U.S.A. California, *Yost & Ritter 364* (OBI).

Native to: New South Wales, South Australia, Southern Queensland, Victoria.

Trees; bark rough, gray, short-fibered, hard; branchlets glaucous. Leaves alternate, concolorous, lanceolate to ovate, dull, blue-green, gray-green or glaucous. Inflorescences compound at branch tips or unbranched umbels in leaf axils; buds sessile, glaucous, spindle-shaped; operculum scar absent. Fruits urn- or barrel-shaped, glaucous; valves enclosed.

4 (6′). Eucalyptus albopurpurea (Boomsma) D. Nicolle, J. Adelaide Bot. Gard. 19: 90. 2000. Basionym: *Eucalyptus lansdowneana* subsp. *albopurpurea* Boomsma, S. Austral. Naturalist 48: 55. 1974.

Common name: purple-flowered mallee.

Voucher: U.S.A. California, *Yost & Ritter 359* (OBI).

Native to: South Australia.

Mallees or shrubs; bark rough, gray, short-fibered, hard. Leaves alternate, concolorous, broadly lanceolate. Inflorescences compound, at branch tips. Operculum scar absent. At anthesis, flowers white, pink, mauve, or purple. Fruits cup- or barrel-shaped; valves enclosed.

6 (9). Eucalyptus amygdalina Labill., Nov. Holl. Pl. 2: 14, tab. 154. 1806.

Common name: black peppermint.

Voucher: Australia, 1902, *F. Walter s.n.* (UC-170397).

Native to: Tasmania.

Trees; bark rough, gray-brown, finely fibrous. Leaves alternate, concolorous, narrowly lanceolate, 0.4–1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences as axillary umbels; buds 11, 15, or more per umbel; operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits sessile or nearly so (pedicels < 0.5 cm long); valves at rim level or enclosed.

5 (17). Eucalyptus angulosa Schauer in Walp., Repert. Bot. Syst. 2(5): 925. 1843.

Common name: ridge-fruited mallee.

Voucher: Western Australia, Swan River Colony, *J. Drummond 4* (type, BM, not seen).

Native to: South Australia, South West Australia.

Mallees or shrubs; lignotuber present; bark smooth. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; buds 3 per umbel, sessile or nearly so, distinctly ribbed, operculum ribbed, operculum scar present. Fruits cylindrical, < 2.5 cm wide; valves enclosed.

7 (8). Eucalyptus annulata Benth., Fl. Austral. 3: 234. 1867.

Common name: open-fruit mallee.

Voucher: Australia, *F. C. Vasek 690319-2* (UC).

Native to: South West Australia.

Mallees; bark smooth; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy; leaf veins obscured by numerous oil glands. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 7 per umbel, sessile. At anthesis, flowers cream to pale yellow. Fruits hemispherical; valves exserted, prominent, stout, tips free at maturity.

7 (9′). Eucalyptus astringens Maiden, Crit. Rev. Eucalyptus 7: 55. 1924. Basionym: *Eucalyptus occidentalis* var. *astringens* Maiden, J. Nat. Hist. Sci. Soc. Western Australia 3: 186. 1911.

Common name: brown mallet.

Voucher: U.S.A. California, *Ritter 63* (OBI).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, sometimes with partly detached flakes, shiny, gray, salmon to brown; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences as axillary umbels; peduncles broad, flattened, and straplike; buds 7 per umbel; operculum equal in length to the hypanthium, operculum scar present. At anthesis, flowers cream to pale yellow. Fruits cup- to bell-shaped; valves exserted, tips free at maturity.

4 (13). Eucalyptus baueriana Schauer in Walp., Repert. Bot. Syst. 2(5): 924. 1843.

Common name: round-leaved box.

Voucher: Australia, *Ritter 84* (OBI).

Native to: New South Wales, Victoria.

Trees; bark rough, gray, short-fibered, hard; branchlets occasionally glaucous. Leaves alternate, concolorous, ovate, glossy. Inflorescences compound, at branch tips. Operculum scar present. At anthesis, flowers white; outer stamens without anthers; stamens shed together in a ring. Fruits urn- or barrel-shaped, glaucous; valves enclosed.

5 (23). Eucalyptus bicostata Maiden, Blakely & Simmonds, Blakely & Simmonds in Simmonds, Trees Other Lands New Zealand, Eucalypts 133. 1927.

Common name: Victorian blue gum.

Voucher: U.S.A. California, *Yost & Ritter 240* (OBI).

Native to: New South Wales, Victoria, South Australia, Tasmania.

Trees; bark smooth, usually with some imperfectly shed rough bark on the basal area of trunk. Leaves alternate, concolorous, lanceolate and sickle-shaped, dark green. Inflorescences as axillary umbels; peduncle absent; buds 3 per umbel, sessile, glaucous; operculum warty, flattened, with a central knob, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile, hemispherical; valves at rim level.

9 (3). Eucalyptus blakelyi Maiden, Crit. Rev. Eucalyptus 4: 43. 1917.

Common name: Blakely's red gum.

Voucher: U.S.A. California, *Ritter 81* (OBI).

Native to: New South Wales, Southern Queensland, Victoria.

Trees; bark smooth, usually with some imperfectly shed rough gray bark on the basal area of trunk, upper limbs smooth; branchlets usually glaucous. Leaves alternate, concolorous, lanceolate; juvenile leaves opposite for fewer than 5 pairs. Inflorescences as axillary umbels; buds 7 per umbel, usually glaucous; operculum longer than the hypanthium, conical to horn-shaped. At anthesis, flowers white. Fruits hemispherical; valves exserted.

3 (22). Eucalyptus botryoides Sm., Trans. Linn. Soc. London 3: 286. 1797.

Common name: southern mahogany.

Voucher: Australia, *Ritter 56* (OBI).

Native to: New South Wales, Victoria. Naturalized: Hawaii, New Zealand, South Australia, South Africa, South West Australia.

Trees; bark rough, thick, gray, fibrous. Leaves alternate, discolorous, broadly lanceolate. Inflorescences axillary umbels; peduncles broad, flattened; buds 7 or more per umbel, sessile; operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits barrel-shaped, sessile; valves enclosed, tips free at maturity.

9 (13). Eucalyptus brassiana S. T. Blake, Austrobaileya 1(1): 1. 1977.

Common name: Cape York red gum.

Voucher: Australia, Queensland, Cooktown, 28 January 1958, *S. T. Blake 20194* (type, BRI, not seen).

Native to: Northern Queensland.

Trees; bark rough, hard, ironbark-like on lower trunk to ca. 3 m, then smooth, gray, white, cream, and yellow above. Leaves alternate, concolorous, lanceolate; juvenile leaves green, entire. Inflorescences axillary umbels; buds 7 per umbel; operculum scar present. At anthesis, flowers white. Fruits hemispherical, pedicellate; disk of fruit steeply ascending; valves exserted.

2 (5) and 9 (11). Eucalyptus bridgesiana R. T. Baker, Proc. Linn. Soc. New South Wales 23: 164. 1898.

Common name: apple box.

Voucher: Australia, *Ritter 102* (OBI).

Native to: New South Wales, Southern Queensland, Victoria. Naturalized: Hawaii, South Africa.

Trees; bark rough, fibrous, sometimes hard and ironbark-like. Juvenile leaves glaucous, crenulate, opposite; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 per umbel; operculum scar present. At anthesis, flowers white. Fruits hemispherical, pedicellate; disk of fruit ascending; valves exserted.

8 (4). Eucalyptus caesia subsp. **caesia** Benth., Fl. Austral. 3: 227. 1867.

Common name: caesia.

Voucher: U.S.A. California, *Yost & Ritter 358* (OBI).

Native to: South West Australia.

Mallees; bark smooth, older bark peeling and rolling in thin vertical strips; branchlets pendulous or upright, glaucous. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 (sometimes 3) per umbel, glaucous; operculum smooth, operculum scar present. At anthesis, the flowers with filaments red or pink with yellow anthers. Fruits urn-shaped; disk of fruit descending; valves at rim level or enclosed.

5 (9). Eucalyptus caesia subsp. **magna** Brooker & Hopper, Nuytsia 4: 117. 1982.

Common name: silver princess.

Voucher: U.S.A. California, *Ritter 119* (OBI).

Native to: South West Australia.

Mallees; bark smooth, older bark peeling and rolling in thin vertical strips; branchlets pendulous, glaucous. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds usually 3 per umbel, glaucous; operculum smooth, operculum scar present. At anthesis, flowers with filaments red or pink with yellow anthers. Fruits urn-shaped; disk of fruit descending; valves at rim level or enclosed.

Eucalyptus caesia subsp. *magna* is more widely cultivated than *E. caesia* subsp. *caesia* and has larger leaves, buds, and fruit.

8 (3). Eucalyptus calycogona Turcz., Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 10: 338. 1852.

Common name: square-fruited mallee.

Voucher: U.S.A. California, *Yost & Ritter 252* (OBI).

Native to: South Australia, South West Australia, Victoria.

Mallees or shrubs; bark smooth, gray; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds usually 7 per umbel, square in cross-section. At anthesis, flowers white, occasionally pink; outer stamens without anthers. Fruits square in cross-section; valves enclosed.

9 (22). Eucalyptus camaldulensis Dehnh., Cat. Pl. Hort. Camald. (ed. 2), 20. 1832.

Common name: red gum or river red gum.

Voucher: U.S.A. California, *Sanders 21982* (CAS).

Native to: North Australia, New South Wales, North West Australia, South Australia, South West Australia, Queensland, Victoria. Naturalized: Argentina, Bangladesh, California, Hawaii, India, Mediterranean Basin, South Australia, South Africa, Zimbabwe.

Trees; bark smooth, not powdery to the touch, usually with some imperfectly shed rough gray bark on the basal area of trunk; branchlet pith without oil glands, often drooping. Juvenile leaves opposite for fewer than 5 pairs; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 per umbel; operculum hemispherical and beaked, equal in length to hypanthium, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

7 (18). Eucalyptus cernua Brooker & Hopper, Nuytsia 14: 342. 2002.

Common name: red-flowered moort.

Voucher: U.S.A. California, *Yost & Ritter 234* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present or absent; bark smooth; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to ovate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 7 per umbel; operculum rounded, narrower than the hypanthium; some or all stamens inflexed in bud (bent downward under operculum). At anthesis, flowers red, yellow, or chartreuse. Fruits sessile, with narrow longitudinal ridges; valves enclosed.

1 (16). Eucalyptus cinerea F. Muell. ex Benth., Fl. Austral. 3: 239. 1867.

Common name: mealy stringybark or argyle apple.

Voucher: U.S.A. California, *Keil 11873-10* (OBI).

Native to: New South Wales, Victoria. Naturalized: Hawaii, New Zealand, South Africa.

Trees; bark rough, brown, thick, fibrous; crown of mature tree composed primarily of juvenile and intermediate leaves. Juvenile leaves opposite, not fused, ovate, glaucous, base wrapping around stem; intermediate leaves opposite, pedicellate, glaucous, ovate to lanceolate. Inflorescences axillary umbels; buds 3 per umbel, diamond-shaped, glaucous. At anthesis, flowers white. Fruits sessile, funnel-shaped; valves exserted.

3 (7). Eucalyptus cladocalyx F. Muell., Linnaea 25(4): 388–389. 1853.

Common name: sugar gum.

Voucher: U.S.A. California, *R. Philbrick B65-44* (CAS).

Native to: South Australia. Naturalized: California, Hawaii, South Africa, South West Australia, Victoria.

Trees; bark smooth, mottled with patches of white, orange, gray, and brown. Leaves alternate, discolorous, shiny, lanceolate to sickle-shaped; leaf oil glands small, obscure. Inflorescences unbranched umbels; buds and fruits born on leafless sections of branchlets; buds 7, 9, or 11 per umbel; operculum rounded, operculum scar present. At anthesis, flowers white. Fruits cylindrical, urn- or barrel-shaped, often ribbed; valves enclosed.

3 (14). Eucalyptus cloeziana F. Muell., Fragm. 11(89): 44–45. 1878.

Common name: gympie messmate.

Voucher: U.S.A. California, 1919, *W. D. Francis s.n.* (UC-206164).

Native to: Queensland.

Trees; bark rough, flaky. Leaves alternate, discolorous, lanceolate. Inflorescences compound, in leaf axils; operculum scar absent. At anthesis, flowers white. Fruits hemispherical; valves at rim level or exserted.

8 (5). Eucalyptus cneorifolia DC., Prodr. 3: 220. 1828.

Common name: Kangaroo Island narrow-leaved mallee.

Voucher: U.S.A. California, *P. G. Wilson 896* (UC).

Native to: South Australia.

Trees or mallees; bark rough, compacted, gray-brown on trunk or lower limbs, smooth and white or gray on upper limbs and branches. Leaves alternate, concolorous, linear to narrowly lanceolate, erect and ascending on the stem, glossy. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, round in cross-section; operculum conical, operculum scar present. Flowers white. Fruits cup-shaped; valves near rim level or slightly exserted.

5 (15), 5 (30), and 6 (18). Eucalyptus coccifera Hook. f., London J. Bot. 6: 477. 1847.

Common name: Tasmanian snow gum.

Voucher: U.S.A. California, *H. Walker 2940* (UC).

Native to: Tasmania.

Trees or mallees; bark smooth; young branches warty, glaucous. Leaves alternate, concolorous, lanceolate to ovate, glossy, with a delicate hook at the tip; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 3, 7, or 9 per umbel, wrinkled and warty, glaucous, round in cross-section; operculum flattened, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits hemispherical, shortly pedicellate, rarely sessile; valves at rim level or enclosed.

7 (6). Eucalyptus conferruminata D. J. Carr & S. G. M. Carr, Austral. J. Bot. 28(5–6): 535. 1980.

Common name: Bald Island marlock.

Voucher: U.S.A. California, *Keil 11873-19* (OBI).

Native to: South West Australia. Naturalized: California, South Africa, Victoria.

Trees or shrubs; lignotuber absent; bark smooth, white and gray; branchlet pith without oil glands; apical bud 1–2.2 cm long, triangular in cross-section. Leaves alternate, concolorous, elliptical. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds more than 7 per umbel, fused at the base; operculum stout, horn-shaped. At anthesis, flowers green or chartreuse. Fruits fused at the base into a woody mass to 4 cm wide; valves exserted, tips connected at maturity.

1 (18′). Eucalyptus conspicua L. A. S. Johnson & K. D. Hill, Telopea 4(2): 235. 1991.

Common name: Gippsland swamp-box.

Voucher: U.S.A. California, *Ritter 34* (OBI).

Native to: New South Wales, Victoria.

Trees; bark rough, brown, thick, fibrous; crown of mature tree composed primarily of juvenile and intermediate leaves. Crown leaves opposite or alternate, concolorous, entire, not fused, ovate to lanceolate, glaucous, sessile and wrapping around stem or petiolate. Inflorescences axillary umbels; buds 7 per umbel, diamond-shaped, glaucous; operculum scar present. At anthesis, flowers white. Fruits sessile, funnel-shaped; valves exserted.

4 (8). Eucalyptus coolabah Blakely & Jacobs, Key Eucalypts 245. 1934.

Common name: coolibah.

Voucher: U.S.A. California, 1945, *M. S. Clemens s.n.* (UC-081390).

Native to: North West Australia, North Australia, South Australia, Queensland, New South Wales.

Trees; bark rough, gray, short-fibered, hard. Leaves alternate, concolorous, lanceolate, dull, blue-green, or gray-green. Inflorescences compound, at branch tips; buds often glaucous; operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

1 (15). Eucalyptus cordata Labill., Nov. Holl. Pl. 2: 13. 1806.

Common name: heart-leaved silver gum.

Voucher: U.S.A. California, *Yost & Ritter 167* (OBI).

Native to: Tasmania.

Trees; bark smooth; branchlets glaucous; crown of mature tree composed primarily of juvenile and intermediate leaves. Crown leaves opposite or alternate, concolorous or slightly discolorous, heart-shaped, or ovate, or lanceolate, base wrapping around the stem, dull, blue-green, glaucous, some leaf margins crenulate. Inflorescences axillary umbels; buds 3 per umbel, sessile, glaucous; operculum scar present. At anthesis, flowers white. Fruits sessile, cup-shaped, ca. 1 cm wide; valves at rim level.

7 (4). Eucalyptus cornuta Labill., Voy. Rech. Pérouse 1: 402, tab. 17. 1800.

Common name: yate.

Voucher: U.S.A. California, *Ritter 35* (OBI).

Native to: South West Australia.

Trees, occasionally mallees; bark rough; branchlet pith glandular, occasionally not glandular. Leaves alternate, concolorous, lanceolate to ovate, glossy. Inflorescences axillary umbels; peduncle flattened; buds elongated, free at the base; operculum horn-shaped, operculum scar present. At anthesis, flowers cream to yellow. Fruits sessile; valves exserted, tips connected at maturity.

5 (13′). Eucalyptus cosmophylla F. Muell., Trans. & Proc. Victorian Inst. Advancem. Sci. 32. 1855.

Common name: cup gum.

Voucher: U.S.A. California, *Yost & Ritter 176* (OBI).

Native to: South Australia.

Mallees, occasionally trees; bark smooth, gray. Leaves alternate, concolorous, broadly lanceolate. Inflorescences axillary umbels; buds 3 per umbel; operculum scar present. At anthesis, flowers white. Fruits sessile, cup-shaped; valves near rim level.

2 (6). Eucalyptus crebra F. Muell., J. Proc. Linn. Soc., Bot. 3: 87. 1859 [1858].

Common name: narrow-leaved ironbark.

Voucher: U.S.A. California, *Ritter 103* (OBI).

Native to: New South Wales, Queensland. Naturalized: Hawaii, South Africa.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs. Leaves alternate, concolorous, narrowly lanceolate, dull, gray-green. Inflorescences compound, at branch tips. Operculum rounded, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup- or barrel-shaped; valves enclosed.

1 (17). Eucalyptus crenulata Blakely & Beuzev., Contr. New South Wales Natl. Herb. 1: 37. 1939.

Common name: Buxton gum.

Voucher: U.S.A. California, *Ritter 46* (OBI).

Native to: Victoria.

Trees; bark rough, compacted, gray, brown, or black; branchlets occasionally glaucous; crown of mature tree composed primarily of juvenile leaves. Crown leaves opposite, sessile, crenulate, not fused, ovate or heart-shaped, glaucous, base wrapping around stem. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, glaucous; operculum scar present. At anthesis, flowers white. Fruits cup-shaped; valves enclosed.

1 (9′). Eucalyptus crucis Maiden, Crit. Rev. Eucalyptus 6(59): 514, pl. 242 (7). 1923.

Common name: Southern Cross silver mallee.

Voucher: U.S.A. California, 1941, *H. W. Sheperd s.n.* (UC-180502).

Native to: South West Australia.

Mallees or shrubs; bark smooth, older bark peeling and rolling in thin vertical strips; branchlets glaucous, round in cross-section; crown of mature tree composed primarily of juvenile leaves. Crown leaves opposite, concolorous, sessile, orbicular or heart-shaped. Inflorescences axillary umbels; buds 7 per umbel, spherical, glaucous; operculum smooth, rounded, operculum scar present. At anthesis, flowers white to pale yellow. Fruits hemispherical, > 1 cm wide; valves exserted.

3 (2). Eucalyptus curtisii Blakely & C. T. White, Proc. Roy. Soc. Queensland 42: 82. 1930 [1931].

Common name: Plunkett mallee.

Voucher: U.S.A. California, *Yost & Ritter 328* (OBI).

Native to: Southern Queensland.

Mallees, rarely small trees; bark smooth, gray. Leaves alternate, discolorous, lanceolate; oil glands obscure or absent from leaves. Inflorescences compound, at branch tips; buds with 4 small persistent sepals; petals not entirely united into an operculum. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, dehiscing by a cap rather than opening by valves.

8 (11) and 8 (24′). Eucalyptus cylindrocarpa Blakely, Key Eucalypts 116. 1934.

Common name: woodline mallee.

Voucher: U.S.A. California, *Ritter JR28* (OBI).

Native to: South West Australia.

Trees or mallees; bark smooth, pinkish, gray, coppery, or occasionally white; branchlet pith glandular. Leaves alternate, concolorous, linear to narrowly lanceolate, glossy. Inflorescences axillary umbels; peduncles slender; buds 7, 9, or 11 per umbel, round in cross-section, pedicellate, smooth; operculum beaked or conical, operculum scar present; stamens inflexed in bud (bent downward under operculum). At anthesis, flowers white. Fruits cylindrical to barrel-shaped; valves enclosed.

7 (11′). Eucalyptus cypellocarpa L. A. S. Johnson, Contr. New South Wales Natl. Herb. 3: 114. 1962.

Common name: monkey gum.

Voucher: U.S.A. California, *R. Coveny & C. Bartlett 5352* (UC).

Native to: New South Wales, Victoria.

Trees; bark smooth, yellowish, gray, cream, or orange-brown; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; peduncles flattened; buds 7 per umbel; operculum beaked or conical, equal in length to the hypanthium, operculum scar present. At anthesis, flowers white. Fruits cylindrical to barrel-shaped; valves enclosed.

5 (26′). Eucalyptus dalrympleana Maiden, Forest Fl. N. S. W. 7: 137. 1920.

Common name: broad-leaved ribbon gum.

Voucher: U.S.A. California, *Yost & Ritter 338* (OBI).

Native to: New South Wales, South Australia, Southern Queensland, Tasmania, Victoria.

Trees; bark smooth, occasionally with short stocking of rough bark; white, gray, or cream, shedding in ribbons. Juvenile leaves ovate to elliptical, dull, blue-green; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 3 per umbel, round in cross-section; operculum conical, smooth, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, disk raised; valves exserted.

9 (3′). Eucalyptus dealbata Schauer in Walp., Repert. Bot. Syst. 2(5): 924. 1843.

Common name: hill red gum.

Voucher: U.S.A. California, *Ritter 88* (OBI).

Native to: New South Wales, Southern Queensland.

Trees; bark smooth, usually with some imperfectly shed rough gray bark on the basal area of trunk, upper limbs smooth; branchlets glaucous. Juvenile leaves opposite for fewer than 5 pairs; adult leaves alternate, concolorous, lanceolate, dull, occasionally blue-green. Inflorescences axillary umbels; buds 7 per umbel, glaucous; operculum equal in length to the hypanthium, conical to horn-shaped, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

3 (9). Eucalyptus deanei Maiden, Proc. Linn. Soc. New South Wales 29: 471. 1904.

Common name: mountain blue gum.

Voucher: Australia, New South Wales, The Valley, Springwood, Apr. 1888, *H. Deane s.n.* (NSW, not seen).

Native to: New South Wales. Naturalized: Hawaii, South Africa.

Trees; bark smooth, occasionally with a short stocking of rough bark at the base. Leaves alternate, discolorous, lanceolate. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel; operculum conical to rounded, operculum scar present. At anthesis, flowers white. Fruits cup-shaped; valves at rim level or slightly exserted.

3 (5). Eucalyptus deglupta Blume, Mus. Bot. 1: 83. 1850.

Common name: rainbow gum or Mindanao gum.

Voucher: U.S.A. California, *E. F. De Vogel 5213* (UC).

Native to: Tropical areas to the north of Australia. Naturalized: Hawaii.

Trees; bark smooth, multicolored, green, lime-green, orange, pink, blue, red, and gray. Leaves alternate, discolorous, lanceolate to ovate. Inflorescences com-

pound, at branch tips. At anthesis, flowers white. Fruits < 0.5 cm wide, hemispherical; valves exserted.

6 (17). Eucalyptus delegatensis R. T. Baker, Proc. Linn. Soc. New South Wales 25: 305. 1900.

Common name: alpine ash.

Voucher: U.S.A. California, *Yost & Ritter 179* (OBI).

Native to: New South Wales, Tasmania, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark rough on lower trunk, finely fibrous, gray or brown, smooth on upper trunk and larger limbs, white or cream. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences as axillary umbels; peduncles round in cross-section; buds 7 to 15 per umbel, often glaucous; operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, hemispherical or barrel-shaped; valves at rim level or enclosed.

9 (16). Eucalyptus dielsii C. A. Gardner, J. Roy. Soc. Western Australia 12: 67. 1927.

Common name: cap-fruited mallet.

Voucher: Australia, *H. Steedman 119723* (UC-1392242).

Native to: South West Australia.

Mallees or small trees; bark smooth, brownish or greenish; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; peduncles round in cross-section; buds 7, occasionally 9 per umbel. At anthesis, flowers yellow or chartreuse. Fruits with a prominent flange around the rim; valves near rim level or exserted.

3 (7′). Eucalyptus diversicolor F. Muell., Fragm. 3(22): 131. 1863.

Common name: karri.

Voucher: U.S.A. California, *Ritter 57* (OBI).

Native to: South West Australia.

Trees; bark smooth, cream, orange, gray, and brown, mottled, shedding in plates and patches. Leaves alternate, discolorous, lanceolate to broadly lanceolate, dull; leaf oil glands obvious. Inflorescences axillary umbels; buds 7 per umbel; operculum rounded to conical. At anthesis, flowers white. Fruits barrel-shaped, smooth; valves enclosed.

6 (12). Eucalyptus dives Schauer in Walp., Repert. Bot. Syst. 2(5): 926. 1843.

Common name: blue peppermint.

Voucher: Australia, *J. H. Maiden 10.98* (UC-19827).

Native to: New South Wales, Victoria.

Trees; bark rough, gray-brown, finely fibrous. Juvenile leaves opposite, sessile, ovate, gray-green to glaucous; adult leaves alternate, concolorous, lanceolate to sickle-shaped, > 1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases tapering evenly, or almost evenly, to the petiole. Inflorescences axillary umbels; buds 11, 15 or more per umbel; operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped; valves at rim level.

5 (5). Eucalyptus dolichorhyncha (Brooker) Brooker & Hopper, Nuytsia 9(1): 57. 1993. Basionym: *Eucalyptus forrestiana* subsp. *dolichorhyncha* Brooker, J. Roy. Soc. Western Australia 56(3): 74. 1973.

Common name: fuchsia gum.

Voucher: Australia, *R. Coveny 5192* (UC).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, pale gray, shedding in ribbons; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, thin, dull. Inflorescences solitary flowers in leaf axils; buds bright red, square in cross-section, with 4 wings, pedicellate; peduncles slender; operculum slender and beaked, operculum scar present. At anthesis, flowers yellow. Fruits square in cross-section, winged; valves enclosed.

8 (11′). Eucalyptus dumosa A. Cunn. ex Oxley, J. Exped. N. S. Wales 63. 1820.

Common name: white mallee.

Voucher: Australia, 1906, *H. B. Williamson s.n.* (UC-872991).

Native to: New South Wales, South Australia, Victoria.

Mallees or shrubs; bark rough on lower parts of trunk and branches; branchlet pith glandular; branchlets green, orange or red, not glaucous. Leaves alternate, concolorous, lanceolate, dull, entire, > 1.5 cm wide, blue-green to gray-green, older leaves can be glossy. Inflorescences axillary umbels; peduncles slender; buds 7 per umbel, pedicellate, cylindrical, round in cross-section; operculum conical or slightly beaked, operculum scar present. At anthesis, flowers white. Fruits cup-shaped to cylindrical, slightly ribbed; valves enclosed or near rim level.

8 (18). Eucalyptus dundasii Maiden, J. & Proc. Roy. Soc. New South Wales, 1915, 49: 309. 1916.

Common name: Dundas blackbutt.

Voucher: U.S.A. California, *Yost & Ritter 290* (OBI).

Native to: South West Australia.

Trees; bark rough on lower trunk, scaly, blackish, smooth on upper trunk and larger limbs, coppery; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to sickle-shaped. Inflorescences axillary umbels; peduncles slender; buds 7 per umbel; operculum beaked, operculum scar present. At anthesis, flowers white. Fruits cylindrical, sessile; valves enclosed.

9 (21). Eucalyptus dunnii Maiden, Proc. Linn. Soc. New South Wales, ser. 2, 30: 336–338. 1905.

Common name: Dunn's white gum.

Voucher: U.S.A. California, *Yost & Ritter 277* (OBI).

Native to: New South Wales, Southern Queensland.

Trees; bark smooth, not powdery to the touch, usually with some imperfectly shed rough gray bark on the basal area of trunk; branchlet pith without oil glands. Juvenile leaves opposite for more than 10 pairs; adult leaves alternate, concolorous or slightly discolorous, lanceolate, with translucent oil glands. Inflorescences axillary umbels; buds 7 per umbel; operculum conical, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

6 (17′). Eucalyptus elata Dehnh., Cat. Pl. Horti Camald. 26. 1829.

Common name: river peppermint.

Voucher: U.S.A. California, 1900, *J. Burtt Davy s.n.* (UC-40989).

Native to: New South Wales, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark rough on lower trunk only, furrowed, compact, brown-black, smooth on upper trunk and larger limbs, white or cream, shed in ribbons. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases tapering evenly, or almost evenly, to the petiole. Inflorescences axillary umbels; peduncles round in cross-section; buds 11 to 30 or more per umbel, green; operculum scar absent. At anthesis, flowers white. Fruits pedicellate, hemispherical or cup-shaped; valves enclosed.

7 (19). Eucalyptus eremophila (Diels) Maiden, J. & Proc. Roy. Soc. New South Wales 54: 71. 1920.
Basionym: *Eucalyptus occidentalis* var. *eremophila* Diels, Bot. Jahrb. Syst. 35: 442. 1904.

Common name: sand mallet.

Voucher: U.S.A. California, *Yost & Ritter 231* (OBI).

Native to: South West Australia.

Mallees or small trees; lignotuber present or absent; bark smooth; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to ovate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike, green; buds 7 per umbel, smooth; operculum conical or horn-shaped; all stamens erect when in bud (not bent under operculum), operculum scar present. At anthesis, flowers white, occasionally pink. Fruits down-turned, cup-shaped; valves enclosed or at rim level.

5 (7). Eucalyptus erythrocorys F. Muell., Fragm. 2(12): 33–34. 1860.

Common name: redcap gum or Illyarrie.

Voucher: U.S.A. California, *Ritter 67* (OBI).

Native to: South West Australia.

Mallees or shrubs; bark smooth, gray, brown. Leaves opposite or slightly alternate (subopposite), concolorous, lanceolate to sickle-shaped, petiolate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and stout; buds 3 per umbel, ridged, with minute sepal teeth; operculum bright red, flattened, ridged with 4 lobes; operculum scar absent. In anthesis, flowers with stamens yellow or chartreuse, in 4 clusters. Fruits $>$ 3 cm wide, 4-lobed; valves enclosed.

5 (13) and 8 (10). Eucalyptus erythronema Turcz., Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg, ser. 2, 10: 337. 1852.

Common name: red-flowered mallee.

Voucher: U.S.A. California, *Ritter 62* (OBI).

Native to: South West Australia.

Mallees, occasionally small trees; bark smooth, pink, brown, burnt red, or white, powdery. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; buds 3 per umbel, occasionally 7; operculum conical, operculum scar present. At anthesis, flowers red to pale yellow. Fruits down-turned, pedicellate, funnel-shaped; valves near rim level or slightly exserted.

3 (24) and 6 (13). Eucalyptus eugenioides Sieber ex Spreng., Syst. Veg. (ed. 16) 4(2): 195. 1827.

Common name: thin-leaved stringybark.

Voucher: U.S.A. California, 1917, *Hill & Metcalf s.n.* (UC-1569427).

Native to: New South Wales, Southern Queensland, Victoria.

Trees; bark rough, gray-brown, fibrous, fissured. Juvenile leaves alternate, petiolate; adult leaves alternate, concolorous or slightly discolorous, lanceolate to sickle-shaped, thin, > 1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases tapering evenly, or almost evenly to the petiole. Inflorescences axillary umbels; buds 9 to 15 per umbel; operculum conical to beaked, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped; valves at rim level, tips free at maturity.

6 (4). Eucalyptus fastigata H. Deane & Maiden, Proc. Linn. Soc. New South Wales 21: 809. 1897.

Common name: brown barrel.

Voucher: U.S.A. California, *Ritter 345* (OBI).

Native to: New South Wales, Victoria. Naturalized: California, New Zealand, South Africa.

Trees; bark rough to the smaller limbs, gray-brown, fibrous. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, sometimes parallel; leaf bases tapering to petiole unevenly (oblique), or occasionally almost evenly to the petiole. Inflorescences paired umbels in leaf axils; buds 11 to 15, or more per umbel; operculum conical or beaked, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped; valves at rim level or slightly exserted.

2 (7). Eucalyptus fibrosa F. Muell., J. Proc. Linn. Soc., Bot. 3: 87. 1859.

Common name: broad-leaved ironbark.

Voucher: U.S.A. California, *Ritter 154* (OBI).

Native to: New South Wales, Queensland.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs. Leaves alternate, concolorous, lanceolate, dull, gray-green. Inflorescences compound, at branch tips. Operculum conical, 1.5× the length of the hypanthium, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup- or barrel-shaped; valves exserted.

8 (13′). Eucalyptus flocktoniae (Maiden) Maiden, J. & Proc. Roy. Soc. New South Wales 49: 316. 1915 [1916].

Common name: merrit.

Voucher: Australia, *C. A. Gardner 1686* (UC).

Native to: South West Australia.

Mallees; bark smooth, cream to coppery; branchlet pith without oil glands; branchlets green, orange, or red, not glaucous. Leaves alternate, concolorous, lanceolate, glossy, entire. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, pedicellate, slightly ribbed, round in cross-section; operculum beaked to horn-shaped, operculum scar present. At anthesis, flowers white to pale yellow. Fruits urn-shaped to barrel-shaped, slightly ribbed; valves appearing enclosed, but occasionally look exserted due to the delicate remnant style tips at the distal end of the valves.

9 (7). Eucalyptus formanii C. A. Gardner, J. Roy. Soc. Western Australia 27: 186. 1942.

Common name: die hardy mallee.

Voucher: U.S.A. California, *Yost, Ritter & Sanders 301* (OBI).

Native to: South West Australia.

Mallees or shrubs, rarely trees; bark rough, wavy, fibrous, brown or gray; branchlets not glaucous; branchlet pith without oil glands. Leaves alternate, concolorous, linear, < 0.5 cm wide, held erect, glossy. Inflorescences axillary umbels; buds 7 or 9 per umbel, pedicellate; operculum conical or beaked, operculum scar present. At anthesis, flowers white. Fruits pedicellate, cup-shaped; valves exserted.

5 (5′). Eucalyptus forrestiana Diels, Bot. Jahrb. Syst. 35: 439. 1904.

Common name: fuchsia gum.

Voucher: U.S.A. California, *Yost & Ritter 139* (OBI).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, pale gray, shedding in ribbons; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, thin, dull. Inflorescences as solitary flowers in leaf axils; peduncles slender; buds bright red, square in cross-section, with 4 wings, pedicellate; operculum flat and disklike, operculum scar present. At anthesis, flowers yellow. Fruits square in cross-section, winged; valves enclosed.

7 (11). Eucalyptus gardneri Maiden, Crit. Rev. Eucalyptus 7(62): 53, pl. 254 (5). 1924.

Common name: blue mallet.

Voucher: Australia, *C. T. White 5287* (UC).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, tan, copper, salmon, brown, shedding in small curls; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, dull. Inflorescences axillary umbels; peduncles flattened; buds 9 or 11 per umbel; operculum horn-shaped, 2 to 3× longer

than the hypanthium, operculum scar present. At anthesis, flowers pale yellow. Fruits cylindrical to barrel-shaped; valves near rim level.

5 (28′). Eucalyptus glaucescens Maiden & Blakely, Crit. Rev. Eucalyptus 8: 56. 1929.

Common name: Tingiringi gum.

Voucher: U.S.A. California, *Yost & Ritter 271* (OBI).

Native to: New South Wales, Victoria.

Trees, rarely mallees; bark rough and fibrous on lower trunk, smooth and shedding in ribbons above; branchlets usually glaucous. Juvenile leaves free, not fused at the base; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 3 per umbel, round in cross-section, glaucous, sessile; operculum smooth, conical, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile, cylindrical or barrel-shaped, 0.8–1.2 cm wide; valves at rim level or enclosed.

5 (2). Eucalyptus globulus Labill., Voy. Rech. Pérouse 1: 153, pl. 13. 1799.

Common name: blue gum, Tasmanian blue gum.

Voucher: U. S. A., California, *Howell 32582* (CAS).

Native to: Tasmania, Victoria. Naturalized: California, Canary Islands, China, Hawaii, India, Jamaica, Peru, Mediterranean Basin, South West Australia, South Africa, Zimbabwe.

Trees; bark smooth usually with imperfectly shed rough bark on the basal area of trunk. Leaves alternate, concolorous, lanceolate and sickle-shaped, dark green. Inflorescences as solitary, glaucous flowers in leaf axils; operculum warty flattened, with a central knob, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile, hemispherical; valves at rim level.

7 (13). Eucalyptus gomphocephala A. Cunn. ex DC., Prod. 3: 220. 1828.

Common name: tuart.

Voucher: U.S.A., California, *Ritter 86* (OBI).

Native to: South West Australia. Naturalized: Hawaii, Mediterranean Basin, South Africa, Victoria.

Trees; bark rough, furrowed, fibrous, flaky, retained on trunk and limbs; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, green; buds 7 per umbel, shaped like a mushroom; operculum hemispherical, wider than the hypanthium, operculum scar present. At anthesis, flowers white. Fruits funnel-shaped to bell-shaped; valves at rim level or slightly exserted.

8 (19) and 9 (5). Eucalyptus goniocalyx F. Muell. ex Miq., Ned. Kruidk. Arch. 4(1): 134. 1856.

Common name: long-leaved box.

Voucher: U.S.A. California, *Yost & Ritter 151* (OBI).

Native to: New South Wales, South Australia, Victoria.

Trees; bark rough, gray and fibrous, to small branches, occasionally small branches smooth; branchlet pith without oil glands; branches not glaucous. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; buds 7 per umbel, sessile; operculum conical, operculum scar present. At anthesis, flowers white. Fruits sessile, cylindrical to barrel-shaped; valves near rim level.

8 (14) and 8 (26). Eucalyptus gracilis F. Muell., 1855. Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 35. 1855.

Common name: white mallee.

Voucher: U.S.A. California, *Yost & Ritter 201* (OBI).

Native to: New South Wales, South Australia, South West Australia, Victoria.

Mallees or trees; bark rough, flaky, fibrous on lower branches and trunk, smooth, white, gray, or brown on the smaller limbs; branches not glaucous; branchlet pith without oil glands. Leaves alternate, concolorous, narrowly lanceolate, glossy, entire, with conspicuous black oil dots. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, round in cross-section, green; operculum rounded or flattened, operculum scar present. At anthesis, flowers white; outer stamens without anthers. Fruits pedicellate, cylindrical to barrel-shaped; valves near rim level.

3 (11). Eucalyptus grandis W. Hill in Anonymous, Cat. Nat. Industr. Prod. Queensland, 25. 1862.

Common name: rose gum.

Voucher: U.S.A. California, *Broder 1472* (CAS).

Native to: New South Wales, Queensland. Naturalized: Arizona, California, Florida, New Zealand, South Australia.

Trees; bark smooth, white, powdery, with a 1–4 m stocking of flaky, gray, rough bark at the base. Leaves alternate, discolorous, lanceolate. Inflorescences axillary umbels; peduncle flattened; buds 7, 9, or 11 per umbel, often glaucous; operculum conical to beaked, operculum scar present. At anthesis, flowers

white. Fruits funnel-shaped, sometimes glaucous; valves 4 or 5, exserted and incurved.

8 (9′). Eucalyptus grossa F. Muell. ex Benth., Fl. Austral. 3: 232. 1867.

Common name: coarse-leaved mallee.

Voucher: U.S.A. California, *Yost & Ritter 356* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark rough, fibrous; branchlets green; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to ovate, glossy, thick. Inflorescences axillary umbels; peduncle stout, downturned; buds 7 per umbel, round in cross-section, green or red, not glaucous, sessile or nearly so; operculum conical, operculum scar present. At anthesis, flowers yellow. Fruits sessile, cylindrical to barrel-shaped; valves enclosed or at rim level.

1 (15′) and 5 (30′). Eucalyptus gunnii Hook. f., London J. Bot. 3: 499. 1844.

Common name: cider gum.

Voucher: U.S.A. California, *Ritter 66* (OBI).

Native to: Tasmania. Naturalized: Mediterranean Basin, New Zealand.

Trees; bark smooth; branchlets glaucous; crown of mature tree composed of juvenile and adult leaves. Juvenile leaves opposite, glaucous, sessile, entire; adult leaves alternate, concolorous, lanceolate to ovate, dull, blue-green, glaucous, petiolate, entire. Inflorescences axillary umbels; peduncles shorter than buds, erect; buds 3 per umbel, sessile, glaucous or green, round in cross-section; operculum smooth, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile or shortly pedicellate, cylindrical or barrel-shaped, $<$ 1 cm wide, shortly pedicellate; valves at rim level or enclosed.

6 (20). Eucalyptus haemastoma Sm., Trans. Linn. Soc. London 3: 286. 1797.

Common name: scribbly gum.

Voucher: U.S.A. California, *Yost & Ritter 190* (OBI).

Native to: New South Wales.

Trees; bark smooth, with prominent scribbles in the wild, but not usually in cultivation; branchlets smooth, green or brown, not glaucous. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 9 to 15 per umbel, round in cross-section; operculum conical, operculum scar absent. At anthesis, flowers white; some outer stamens without anthers. Fruits hemispherical, shortly pedicellate, 0.9 $\times$ 0.9 cm; valves near rim level.

The conspicuous bark scribbles are zigzag tunnels left by larvae of the scribbly gum moth (*Ogmograptis scribula* Meyrick) known from the Australian Capital Territory, New South Wales, and Queensland. Moth scribbles occur in five native *Eucalyptus* species, which include *E. rossii* R. T. Baker & H. G. Sm. and *E. sclerophylla* (Blakely) L. A. S. Johnson & Blaxell, as well as *E. pauciflora* and *E. racemosa* Cav., the latter pair treated herein as naturalized species.

7 (18′) and 8 (6). Eucalyptus incrassata Labill., Nov. Holl. Pl. 2: 2. 1806.

Common name: ridge-fruited mallee.

Voucher: U.S.A. California, *A. C. Sanders 12065* (UC).

Native to: New South Wales, South Australia, South West Australia, Victoria.

Mallees or shrubs; lignotuber present; bark smooth; branchlet pith usually glandular. Leaves alternate, concolorous, lanceolate, glossy, usually with leaf-margin lenticels (Neish et al., 1995) as denticulations along the blade edges. Inflorescences axillary umbels; peduncle flattened, sometimes only slightly so, green; buds 7 per umbel, ribbed; operculum conical to beaked, same width as the hypanthium, operculum scar present. At anthesis, flowers white, occasionally pale yellow, pink, or red. Fruits ribbed; valves enclosed.

4 (16′). Eucalyptus intertexta R. T. Baker, Proc. Linn. Soc. New South Wales 25: 308. 1900.

Common name: gum coolibah.

Voucher: U.S.A. California, *Ritter 94* (OBI).

Native to: North Australia, New South Wales, North West Australia, South Australia, South West Australia, Southern Queensland.

Trees; bark rough, gray, short-fibered, hard, rough bark extending only to base of larger branches, bark of small branches smooth. Leaves alternate, concolorous, lanceolate, dull, blue-green; leaf oil glands and intramarginal leaf veins obscure or absent. Inflorescences compound, at branch tips; buds with operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, barrel-shaped, or hemispherical; valves enclosed.

5 (18′). Eucalyptus kingsmillii (Maiden) Maiden & Blakely, Crit. Revis. Eucalyptus 8: 43. 1929.
Basionym: *Eucalyptus pyriformis* var. *kingsmillii*

Maiden, J. & Proc. Roy. Soc. New South Wales 52: 508. 1919.

Common name: Kingsmill's mallee.

Voucher: Australia, July 1918, *W. Kingsmill s.n.* (isotype, UC-437558).

Native to: North West Australia, South West Australia.

Mallees or shrubs; lignotuber present; bark rough at the base and smooth above, or sometimes completely smooth; branchlet piths without oil glands. Leaves alternate, concolorous, lanceolate, dull. Inflorescences unbranched, pendulous, umbels in leaf axils; peduncles slender; buds 3 per umbel, pedicellate, distinctly ribbed; operculum conical to beaked, ribbed, operculum scar present. At anthesis, flowers white. Fruits hemispherical, with > 5 prominent ridges; disk of fruit raised; valves exserted.

8 (13) and 8 (20). Eucalyptus kitsoniana Maiden, Crit. Rev. Eucalyptus 3: 164. 1916.

Common name: Gippsland mallee.

Voucher: U.S.A. California, *Yost & Ritter 263* (OBI).

Native to: Victoria. Naturalized: California.

Mallees or trees; bark smooth, coppery, shedding in ribbons; branchlet pith without oil glands; branchlets green, orange, or red, not glaucous. Leaves alternate, concolorous, lanceolate, glossy, entire. Inflorescences axillary umbels, often subtended by a prominent bract; buds 7 per umbel, sessile, round in cross-section, green; operculum rounded or conical, operculum scar present. At anthesis, flowers white. Fruits cup-shaped, sessile; valves enclosed or near rim level.

1 (9). Eucalyptus kruseana F. Muell., Australas. J. Pharm. 10: 233. 1895.

Common name: bookleaf mallee.

Voucher: U.S.A. California, *Yost & Ritter 308* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark rough at the base and smooth above; branchlets glaucous, round in cross-section; branchlet pith glandular; crown of mature tree composed primarily of juvenile leaves. Crown leaves alternate, or nearly opposite, concolorous, sessile, not fused, orbicular or heart-shaped, wrapping around the stem. Inflorescences axillary umbels; buds 7 per umbel, glaucous; operculum smooth, conical, operculum scar present. At anthesis, flowers yellow to chartreuse. Fruits barrel-shaped, < 0.75 cm wide; valves at rim level.

4 (6). Eucalyptus lansdowneana F. Muell. & J. E. Br., For. Fl. S. Australia 9, t. 31. 1890.

Common name: red-flowered mallee box.

Voucher: U.S.A. California, *Yost & Ritter 297* (OBI).

Native to: South Australia.

Mallees or shrubs; bark rough, gray, fibrous, smooth, and coppery on smaller limbs. Leaves alternate, concolorous, lanceolate. Inflorescences compound, at branch tips; buds with operculum conical or rounded, operculum scar absent. At anthesis, flowers red to mauve to pink. Fruits barrel-shaped; valves enclosed.

4 (15′). Eucalyptus largiflorens F. Muell., Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 34. 1855.

Common name: black box.

Voucher: U.S.A. California, 1912, *F. Walter s.n.* (UC-170420).

Native to: New South Wales, Southern Queensland, South Australia, Victoria.

Trees; bark gray, short-fibered, hard, rough to the smallest branches. Leaves alternate, concolorous, lanceolate. Inflorescences compound, at branch tips; buds with operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup- or barrel-shaped, glaucous; valves enclosed.

7 (6′). Eucalyptus lehmannii (Schauer) Benth., Fl. Austral. 3: 233. 1867. Basionym: *Symphyomyrtus lehmannii* Schauer in Lehm., Pl. Preiss. 1(1): 127. 1844.

Common name: bushy yate.

Voucher: U.S.A. California, *Ritter 21* (OBI).

Native to: South West Australia.

Trees or mallees; lignotuber present; bark smooth, white and gray; branchlet pith without oil glands; apical bud < 1 cm long, not triangular. Leaves alternate, concolorous, elliptical. Inflorescences axillary umbels; peduncles broad, flattened, and strap-like; buds more than 7 per umbel, fused at the base; operculum slender, horn-shaped; operculum scar present but hard to see. At anthesis, flowers chartreuse. Fruits fused at the base into a woody mass up to 4 cm wide; valves exserted, tips connected at maturity.

Plants often known and sold as *Eucalyptus lehmannii* are actually *E. conferruminata*.

8 (28′). Eucalyptus lesouefii Maiden, Crit. Rev. Eucalyptus 2: 187. 1912.

Common name: Goldfields' blackbutt.

Voucher: U.S.A. California, 1911, *Mrs. Cleland s.n.* (UC-194860).

Native to: South West Australia.

Trees; bark rough, flaky, dark, fibrous on lower trunk, smooth, brown or coppery above; branches often glaucous; branchlet pith glandular. Leaves alternate, concolorous, narrowly lanceolate. Inflorescences axillary umbels; buds 7 per umbel, diamond-shaped, with prominent ribs, glaucous; operculum conical, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cup-shaped, ribbed, glaucous; valves near rim level.

5 (20). Eucalyptus leucoxylon F. Muell., Trans. & Proc. Victorian Inst. Advancem. Sci. 1: 33–34. 1855.

Common name: white ironbark.

Voucher: U.S.A. California, *Landrum 10965* (OBI).

Native to: New South Wales, South Australia, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark smooth, white, sometimes with incompletely shed, shaggy bark at the base. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 3 per umbel; operculum beaked, operculum scar absent. At anthesis, flowers white, red, pink, yellow, or occasionally orange; outer stamens without anthers. Fruits pedicellate, cup- or barrel-shaped; valves enclosed.

5 (19). Eucalyptus longifolia Link, Enum. Hort. Berol. Alt. 2: 29. 1822.

Common name: woollybutt.

Voucher: U.S.A. California, *Ritter 51* (OBI).

Native to: New South Wales. Naturalized: California, South Africa.

Trees; bark rough, furrowed, retained on trunk and limbs. Leaves alternate, concolorous, lanceolate to sickle-shaped. Inflorescences unbranched, pendulous, umbels, in leaf axils; buds 3 per umbel; operculum conical, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cup-shaped; valves near rim level.

8 (9) and 8 (27). Eucalyptus loxophleba Benth., Fl. Austral. 3: 252. 1867.

Common name: York gum.

Voucher: U.S.A. California, *Yost & Ritter 323* (OBI).

Native to: South West Australia.

Trees or mallees; bark rough to the smallest branches; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to sickle-shaped, glossy. Inflorescences axillary umbels; peduncle slender, upright; buds 7, 9, or 11 per umbel, pedicellate, round in cross-section, green; operculum rounded, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, funnel-shaped; valves enclosed.

9 (10). Eucalyptus macarthurii H. Deane & Maiden, Proc. Linn. Soc. New South Wales, ser. 2, 24: 448. 1899.

Common name: Paddy's River box.

Voucher: U.S.A. California, *Ritter 232* (OBI).

Native to: New South Wales. Naturalized: California, New Zealand, South Africa.

Trees; bark rough, loosely fibrous, fissured, brown or gray, shed as ribbons from the upper limbs; branches not glaucous. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 per umbel, shortly pedicellate, occasionally sessile, operculum conical to beaked, operculum scar present. At anthesis, flowers white. Fruits sessile or pedicellate, funnel- or bell-shaped; disk of fruit flat or slightly raised, not prominent; valves exserted just beyond rim level.

7 (16). Eucalyptus macrandra F. Muell. ex Benth., Fl. Austral. 3: 235. 1867.

Common name: river yate.

Voucher: U.S.A. California, *Ritter 19* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark smooth, coppery, gray, salmon; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike, green; buds 11 or more per umbel; operculum horn-shaped, operculum scar present. At anthesis, flowers yellow. Fruits cup- or barrel-shaped; valves at rim level, tips free.

1 (11′). Eucalyptus macrocarpa Hook., Icon. Pl. 5: t. 405–407. 1841.

Common name: mottlecah.

Voucher: U.S.A. California, *Yost & Ritter 378* (OBI).

Native to: South West Australia.

Mallees or shrubs; bark smooth, shedding in ribbons; branchlets glaucous, round in cross-section; crown of mature tree composed primarily of juvenile leaves. Crown leaves opposite, concolorous, sessile, orbicular or heart-shaped, wrapping around the stem, not fused. Inflorescences solitary, glaucous, in leaf axils; peduncle stout; buds sessile or nearly so, spherical, glaucous; operculum smooth, conical,

beaked, operculum scar present. At anthesis, flowers red. Fruits sessile, saucer- to funnel-shaped; valves exserted.

7 (2). Eucalyptus maidenii (F. Muell.) Kirkpatr., Proc. Linn. Soc. New South Wales, ser. 2, 4: 1020, pl. 28, 29. 1890.

Common name: Maiden's gum.

Voucher: U.S.A. California, *Yost & Ritter 214* (OBI).

Native to: New South Wales, Victoria.

Trees; bark smooth, usually with imperfectly shed rough bark on the basal area of trunk. Leaves alternate, concolorous, lanceolate and sickle-shaped, dark green. Inflorescences axillary umbels; peduncle stout, angled; buds 7 per umbel, sessile, glaucous; operculum warty, flattened, with a central knob, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile, funnel-shaped; valves exserted.

9 (8′). Eucalyptus mannensis Boomsma, Trans. & Proc. Roy. Soc. South Australia 88: 115. 1964.

Common name: Mann Range mallee.

Voucher: Australia, 33 km N of Angas Downs Homestead, Northern Territory, 15 Oct. 1957, *G. M. Chippendale & L. A. S. Johnson 3986* (type, AD, not seen).

Native to: South West Australia, North Australia, South Australia.

Mallees or shrubs; lignotuber present; bark rough, fibrous, brown or gray; branchlets not glaucous; branchlet pith without oil glands. Leaves alternate, concolorous, narrowly lanceolate, > 0.75 cm wide, glossy. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, pedicellate; operculum conical to rounded, operculum scar present. At anthesis, flowers white. Fruits pedicellate, hemispherical; valves exserted.

9 (19). Eucalyptus mannifera Mudie, Trans. Med. Bot. Soc. 1(3): 24. 1834.

Common name: brittle gum or red spotted gum.

Voucher: U.S.A. California, *Ritter 226* (OBI).

Native to: New South Wales, Victoria. Naturalized: California.

Trees; bark smooth, powdery to the touch, white, gray, mottled; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, narrowly lanceolate, sickle-shaped, dull, bluish green. Inflorescences axillary umbels; buds 7 per umbel; operculum conical to beaked, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

3 (25). Eucalyptus marginata Donn ex Sm., Trans. Linn. Soc. London 6: 302. 1802.

Common name: jarrah.

Voucher: U.S.A. California, 1896, *J. H. Barber s.n.* (UC-41048).

Native to: South West Australia. Naturalized: Hawaii, South Africa.

Trees; bark rough, fibrous. Leaves alternate, discolorous, distinctly lighter on the underside, leathery, lanceolate to sickle-shaped. Inflorescences axillary umbels; peduncles slender, round in cross-section; buds 7 to 13 per umbel, green; operculum conical to horn-shaped, operculum scar absent. At anthesis, flowers white; outer stamens erect under operculum when in bud, all stamens with anthers. Fruits > 1 cm wide, globe- to barrel-shaped; valves at rim level or enclosed, tips free at maturity.

7 (7′). Eucalyptus megacornuta C. A. Gardner, J. Roy. Soc. Western Australia 27: 184. 1942.

Common name: warted yate.

Voucher: U.S.A. California, *Yost & Ritter 193* (OBI).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 3 or 7 per umbel, free at the base, green; operculum warty, operculum scar present. At anthesis, flowers yellow to chartreuse. Fruits sessile, free at the base, funnel- to bell-shaped, valves exserted, tips connected at maturity.

1 (3) and 2 (1). Eucalyptus melanophloia F. Muell., J. Proc. Linn. Soc., Bot. 3: 93. 1859.

Common name: silver-leaved ironbark.

Voucher: U.S.A. California, *Yost & Ritter 173* (OBI).

Native to: North Australia, New South Wales, Queensland.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs; crown of mature tree composed primarily of juvenile leaves. Juvenile leaves opposite, sessile, ovate, concolorous, glaucous, gray-green. Inflorescences compound, at branch tips; buds with operculum conical, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, glaucous; valves exserted.

6 (2) and 8 (26′). Eucalyptus melliodora Schauer in Walp., Repert. Bot. Syst. 2(5): 924. 1843.

Common name: honey box.

Voucher: U.S.A. California, *Yost & Ritter 242* (OBI).

Native to: New South Wales, Southern Queensland, Victoria.

Trees; bark rough, fibrous on lower branches and trunk, sometimes rough over the entire trunk, sometimes smooth on the smaller limbs, yellow-brown; branches not glaucous; branchlet pith without oil glands. Leaves alternate, concolorous, narrowly lanceolate to lanceolate, dull, entire. Inflorescences axillary umbels; buds 7 per umbel, round in cross-section, green; operculum rounded or conical, operculum scar absent. At anthesis, flowers white; outer stamens without anthers. Fruits pedicellate, hemispherical; valves enclosed or near rim level.

4 (11′). Eucalyptus microcarpa (Maiden) Maiden, Crit. Rev. Eucalyptus 6(8): 438. 1923. Basionym: *Eucalyptus hemiphloia* var. *microcarpa* Maiden, Trans. & Proc. Roy. Soc. South Australia 26: 11. 1902.

Common name: inland box.

Voucher: Australia, 1917, *J. L. Boorman s.n.* (UC-437482).

Native to: New South Wales, South Australia, Southern Queensland, Victoria.

Trees; bark rough, gray, short-fibered, hard. Leaves alternate, concolorous, lanceolate. Inflorescences compound, at branch tips; buds green, straight; operculum scar absent. Flowers white; all stamens with anthers. Fruits cylindrical or barrel-shaped; valves enclosed or near the fruit rim.

3 (14′). Eucalyptus microcorys F. Muell., Fragm. 2(12): 50. 1860.

Common name: tallowwood.

Voucher: U.S.A. California, *Yost & Ritter 292* (OBI).

Native to: New South Wales, Southern Queensland. Naturalized: Hawaii, South Africa, Sri Lanka, South West Australia, Zimbabwe.

Trees; bark rough, thick, fibrous. Leaves alternate, discolorous, lanceolate. Inflorescences compound, at branch tips; buds club-shaped; operculum scar present. At anthesis, flowers white; stamens in 4 clusters, outer ones without anthers. Fruits funnel-shaped; valves slightly exserted or at rim level.

4 (16). Eucalyptus microtheca F. Muell., J. Proc. Linn. Soc., Bot. 3: 87. 1859.

Common name: tropical coolibah.

Voucher: U.S.A. California, *L. R. Landrum 11295* (OBI).

Native to: North Australia, North West Australia, Queensland. Naturalized: Arizona.

Trees; bark rough, light gray, short-fibered, hard, fissured, rough bark extending only to base of larger branches, bark of small branches smooth. Leaves alternate, concolorous, lanceolate; oil glands obvious; intramarginal leaf vein present. Inflorescences compound, at branch tips; buds with operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits globose to funnel-shaped, sometimes glaucous; valves slightly exserted or at rim level.

3 (21). Eucalyptus miniata Schauer in Walp., Repert. Bot. Syst. 2: 925. 1843.

Common name: Darwin woollybutt.

Voucher: Australia, *L. A. Craven 4058* (UC).

Native to: North Australia, Northern Queensland, North West Australia.

Trees; bark rough, papery, fibrous, brown on most of the trunk; upper trunk and branches with smooth, white bark; branchlets glaucous. Leaves alternate, discolorous, broadly lanceolate. Inflorescences axillary umbels; buds 7 per umbel, glaucous, ribbed; operculum rounded or conical, operculum scar present. At anthesis, flowers orange; all stamens with anthers. Fruits cylindrical or barrel-shaped, sessile or nearly so, glaucous; valves enclosed, tips free at maturity.

5 (10). Eucalyptus morrisii R. T. Baker, Proc. Linn. Soc. New South Wales 25: 312. 1900.

Common name: gray mallee.

Voucher: U.S.A. California, *Yost & Ritter 327* (OBI).

Native to: New South Wales.

Mallees, occasional trees; bark rough, fibrous, gray. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds usually 3 per umbel, green; operculum conical, smooth, green, operculum scar present. At anthesis, flowers white. Fruits globose; disk of fruit raised and convex; valves strongly exserted.

3 (24′) and 6 (13′). Eucalyptus muelleriana A. W. Howitt, Trans. Roy. Soc. Victoria 2(1): 89–91. 1890 [Apr. 1891].

Common name: yellow stringybark.

Voucher: U.S.A. California, 1927, *H. B. Williamson s.n.* (UC-873004).

Native to: New South Wales, Victoria. Naturalized: New Zealand, South Africa, South West Australia.

Trees; bark rough, fibrous, brown. Juvenile leaves alternate, petiolate; adult leaves alternate, slightly discolorous or concolorous, lanceolate, leathery, > 1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases tapering evenly, or almost evenly to the petiole. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel; operculum rounded, operculum scar absent. Flowers white; all stamens with anthers. Fruits pedicellate; valves at rim level or slightly exserted, tips free at maturity.

1 (7′) and 1 (18). Eucalyptus neglecta Maiden, Vict. Naturalist 21: 114. 1904.

Common name: Omeo gum.

Voucher: U.S.A. California, *Yost & Ritter 156* (OBI).

Native to: Victoria.

Trees or mallees; bark rough, brown, fibrous; young stems square in cross-section; crown of mature tree composed primarily of juvenile and intermediate leaves, with occasional adult leaves. Juvenile leaves opposite or alternate, sessile, entire, not fused, ovate, glaucous, base wrapping around stem; intermediate and adult leaves opposite or alternate, entire, pedicellate, glaucous, ovate to lanceolate. Inflorescences axillary umbels; buds 7 to 15 per umbel, oval, sessile, glaucous. At anthesis, flowers white. Fruits sessile, cup-shaped; valves exserted or near rim level.

9 (14). Eucalyptus nicholii Maiden & Blakely, Crit. Rev. Eucalyptus 8: 52. 1929.

Common name: narrow-leaved black peppermint.

Voucher: U.S.A. California, *Ritter 27* (OBI).

Native to: New South Wales.

Trees; bark rough, brown, fibrous to the smallest branches, not shedding in ribbons from smaller branches. Juvenile leaves green or grayish green, linear to narrowly lanceolate, sessile or shortly petioled, entire; adult leaves alternate, concolorous, narrowly lanceolate. Inflorescences axillary umbels; buds 7 per umbel; operculum scar present. At anthesis, flowers white. Fruits pedicellate, hemispherical; disk of fruit thin, slightly ascending; valves exserted.

8 (20′). Eucalyptus nitens (H. Deane & Maiden) Maiden, Crit. Rev. Eucalyptus 2: 273. 1913. Basionym: *Eucalyptus goniocalyx* var. *nitens* H. Deane & Maiden, Proc. Linn. Soc. New South Wales 24: 462. 1899.

Common name: silvertop.

Voucher: U.S.A. California, *Yost & Ritter 227* (OBI).

Native to: New South Wales, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark smooth, pale gray or cream, occasionally with a rough stocking at the base, shed in ribbons from upper branches; branchlet pith without oil glands; branchlets green, orange or red, not glaucous. Leaves alternate, concolorous, lanceolate to sickle-shaped, glossy. Inflorescences axillary umbels; buds 7 per umbel, sessile, round in cross-section, green; operculum conical, operculum scar present. At anthesis, flowers white. Fruits cup- to barrel-shaped, sessile; valves enclosed or near rim level.

7 (21′). Eucalyptus nutans F. Muell., Fragm. 3(23): 152. 1863.

Common name: red-flowered moort.

Voucher: U.S.A. California, *Yost & Ritter 288* (OBI).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, shiny, gray; branchlet pith glandular. Leaves alternate, concolorous, ovate to elliptical, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 7 per umbel, ridged or winged, sessile; horn-shaped, smooth, narrower than and same length as the hypanthium, operculum scar present. At anthesis, flowers red; all stamens erect when in bud (not bent under operculum). Fruits sessile, with narrow longitudinal ridges; valves 5 or 6, enclosed.

6 (10). Eucalyptus obliqua L'Hér., Sert. Angl. 18. 1788 [1789].

Common name: messmate stringybark.

Voucher: U.S.A. California, *Ritter 118* (OBI).

Native to: New South Wales, South Australia, Southern Queensland, Tasmania, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark rough, fibrous, brown. Juvenile leaves pendulous, usually > 6 cm wide, glossy, green, petiolate; adult leaves alternate, concolorous, lanceolate, > 1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases oblique. Inflorescences axillary umbels; buds 11 to 15 or more per umbel; operculum conical to rounded, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate; cup- or barrel-shaped, valves at rim level or enclosed.

7 (9). Eucalyptus occidentalis Endl., Enum. Pl. 49. 1837.

Common name: flat-topped yate.

Voucher: U.S.A. California, 1896, *J. H. Barber s.n.* (UC-41063).

Native to: South West Australia. Naturalized: South Africa, Victoria.

Trees; lignotuber present; bark rough at the base, fibrous, black to gray, smooth bark on upper limbs shedding in strips leaving smooth white or gray bark; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences unbranched, pendulous umbels, in leaf axils; peduncles broad, flattened; buds 7, 9, 11, or 13 per umbel; operculum 1.5 to 2.5× longer than the hypanthium, operculum scar present. At anthesis, flowers cream to pale yellow. Fruits bell-shaped; valves exserted, tips free at maturity.

4 (11). Eucalyptus ochrophloia F. Muell., Fragm. 11(89): 36–37. 1878.

Common name: napunyah.

Voucher: U.S.A. California, *Yost & Ritter 377* (OBI).

Native to: New South Wales, Southern Queensland.

Trees; bark rough, scaly, gray to black, short-fibered, hard on trunk, smooth, coppery on upper limbs and branches. Leaves alternate, concolorous, lanceolate, glossy. Inflorescences compound, at branch tips; buds often curved, spindle-shaped; operculum scar absent. At anthesis, flowers white; outer stamens without anthers. Fruits cylindrical to barrel-shaped; valves enclosed.

9 (8). Eucalyptus oleosa F. Muell. ex Miq., Ned. Kruidk. Arch. 4(1): 127. 1856.

Common name: red morrell.

Voucher: U.S.A. California, *Yost & Ritter 317* (OBI).

Native to: New South Wales, South Australia, South West Australia, Victoria.

Mallees or shrubs; lignotuber present; bark rough, fibrous, flaky, brown or gray; branchlets not glaucous; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate to narrowly lanceolate, > 0.75 cm wide, glossy. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, pedicellate; operculum rounded, operculum scar present. At anthesis, flowers white. Fruits pedicellate, hemispherical; valves exserted, needle-like and fragile.

6 (15). Eucalyptus olsenii L. A. S. Johnson & Blaxell, Telopea 1: 395. 1980.

Common name: Olsen's gum or Woila gum.

Voucher: Australia, New South Wales, Dampier trig., E of Big Badja Hill, 13 June 1972, *H. Fairlie-Cuninghame s.n.* (type, NSW, not seen).

Native to: New South Wales.

Trees; bark smooth, white to gray, rough on lower trunk, fibrous, flaky, gray to brown. Leaves alternate, concolorous, lanceolate; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 7 per umbel, ribbed, scaly; operculum beaked, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits sessile or pedicel < 0.4 cm long; valves enclosed.

9 (2). Eucalyptus orbifolia F. Muell., Fragm. 5(33): 50. 1865.

Common name: round-leaved mallee.

Voucher: U.S.A. California, *Yost & Ritter 142* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark rough and flaky on larger branches, otherwise peeling and rolling in thin vertical strips, reddish brown; branchlets glaucous. Leaves alternate, concolorous, ovate to elliptical. Inflorescences axillary umbels; buds 7 (occasionally 3) per umbel, glaucous, globular; operculum, rounded to conical, operculum scar present. At anthesis, flowers yellow to cream. Fruits pedicellate, glaucous, hemispherical, globose to funnel-shaped; valves exserted.

9 (20). Eucalyptus ovata Labill., Nov. Holl. Pl. 2: 13. 1806.

Common name: black gum or swamp gum.

Voucher: U.S.A. California, *Huber 1203* (CAS).

Native to: New South Wales, South Australia, Tasmania, Victoria. Naturalized: California, New Zealand.

Trees; bark smooth, usually not powdery to the touch, usually with some imperfectly shed rough gray bark on the basal area of trunk; branchlet pith without oil glands. Juvenile leaves opposite for fewer than 5 pairs; adult leaves alternate, concolorous, lanceolate, broadly lanceolate to ovate, often with wavy or undulate margins. Inflorescences axillary umbels; buds 7 per umbel, pedicellate, green; operculum conical, operculum scar present. At anthesis, flowers white. Fruits funnel-shaped; valves at rim level or slightly exserted.

2 (3). Eucalyptus paniculata Sm., Trans. Linn. Soc. London 3: 287–288. 1797.

Common name: gray ironbark.

Voucher: U.S.A. California, *Ritter 104* (OBI).

Native to: New South Wales. Naturalized: Hawaii, South Africa, Zimbabwe.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs. Leaves alternate, discolorous, lanceolate, dull, gray-green. Inflorescences compound, at branch tips; buds with operculum conical, operculum scar present. At anthesis, flowers white; outer stamens without anthers. Fruits cup- to funnel-shaped; valves enclosed.

8 (17). Eucalyptus parvula L. A. S. Johnson & K. D. Hill, Telopea 4(2): 233. 1991.

Common name: small-leaved gum.

Voucher: U.S.A. California, *McClintock s.n.* (CAS-474279).

Native to: New South Wales. Naturalized: California.

Trees; bark smooth, gray, shedding in ribbons, usually with some imperfectly shed rough gray bark on the basal area of trunk; branchlet pith without oil glands; branchlets green, orange, or red, not glaucous; crown of mature trees usually with juvenile, intermediate, and adult leaves. Crown leaves alternate or opposite, concolorous, elliptical, ovate to lanceolate. Inflorescences axillary umbels; buds 7 per umbel, sessile, round in cross-section, green; operculum conical, operculum scar present. At anthesis, flowers white. Fruits cup-shaped, sessile; valves enclosed or near rim level.

6 (6). Eucalyptus pauciflora Sieber ex Spreng., Syst. Veg. (ed. 16) 4(2): 195. 1827.

Common name: snow gum.

Voucher: U.S.A. California, *Yost & Ritter 182* (OBI).

Native to: New South Wales, South Australia, Southern Queensland, Tasmania, Victoria.

Trees; bark smooth, white, cream, and gray; branchlets sometimes glaucous. Leaves alternate, concolorous, lanceolate, glossy; leaf side veins parallel or nearly parallel. Inflorescences axillary umbels; buds 9 to 15 per umbel, club-shaped, rounded, sometimes warty; operculum conical and beaked, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits sessile or nearly so, hemispherical, sometimes glaucous; valves at rim level or enclosed.

3 (20). Eucalyptus pellita F. Muell., Fragm. 4(30): 159–160. 1864 [Sep. 1863–Nov. 1864].

Common name: large-fruited red mahogany.

Voucher: U.S.A. California, *Ritter 112* (OBI).

Native to: Northern Queensland.

Trees; bark rough, thick, fibrous, reddish brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences as axillary umbels; buds 7 or more per umbel; operculum conical, slightly beaked, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cup- to funnel-shaped, with a broad ring on top, > 1.4 cm wide; disk of fruit flat; valves exserted, tips free at maturity.

1 (2) and 5 (28). Eucalyptus perriniana F. Muell. ex Rodway, Pap. & Proc. Roy. Soc. Tasmania 1893: 181. 1894. TYPE: Tasmania. N of Hamilton, May 1892, *L. Rodway s.n.* (lectotype, designated by Bean [2010: 519], HO-16178).

Common name: spinning gum.

Voucher: U.S.A. California, *Yost & Ritter 228* (OBI).

Native to: New South Wales, Tasmania, Victoria.

Trees; bark smooth, gray, white, shedding in ribbons; branchlets glaucous; crown of mature trees with juvenile and adult leaves. Juvenile leaves opposite, glaucous, fused at the base forming a ring; adult leaves alternate or opposite, concolorous, ovate to broadly lanceolate, glaucous. Inflorescences axillary umbels; buds 3 per umbel, round in cross-section, glaucous, sessile or pedicel < 0.2 cm; operculum smooth, rounded and slightly beaked, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits sessile or shortly pedicellate, cylindrical or cup-shaped, glaucous, 0.5–0.8 cm wide; valves at rim level.

6 (16). Eucalyptus pilularis Sm., Trans. Linn. Soc. London 2: 284. 1797.

Common name: blackbutt.

Voucher: U.S.A. California, *Forestry Sta. Santa Monica s.n.* (UC-1569450).

Native to: New South Wales, Southern Queensland. Naturalized: Hawaii, New Zealand, South Africa.

Trees; bark rough on lower trunk, finely fibrous, gray or brown, smooth on upper trunk and larger limbs, white or cream. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; peduncles flattened; buds 7 to 15 per umbel; operculum conical and beaked, operculum scar absent. In anthesis, flowers white; all stamens with anthers. Fruits pedicellate, hemispherical to globose; valves at rim level or enclosed.

7 (21). Eucalyptus platypus Hook., Hooker's Icon. Pl. 9: tab. 849. 1852.

Common name: moort.

Voucher: U.S.A. California, *Yost & Ritter 286* (OBI).

Native to: South West Australia. Naturalized: California, South Africa.

Small trees or shrubs, lacking a lignotuber; bark smooth, gray to coppery; branchlet pith glandular. Leaves alternate, concolorous, orbicular to elliptical, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike, green; buds 7 per umbel, ridged or winged; operculum horn-shaped, 1.5 to 3× longer than the hypanthium, operculum scar present. At anthesis, flowers yellow; all stamens erect when in bud (not bent under operculum). Fruits sessile, with narrow longitudinal ridges; valves 4, enclosed.

1 (7). Eucalyptus pleurocarpa Schauer in Lehm., Pl. Preiss. 1(1): 132. 1844–1845 [1844].

Common name: tallerack.

Voucher: U.S.A. California, *Yost & Ritter 191* (OBI).

Native to: South West Australia.

Mallees; bark smooth, gray; branchlets glaucous, pith glandular; stems square in cross-section. Crown leaves opposite or nearly opposite, petiolate, entire, not fused, ovate to elliptical, glaucous. Inflorescences axillary umbels; peduncles flattened; buds 3 per umbel, pedicellate, 4-angled, glaucous. At anthesis, flowers white to cream. Fruits pedicellate, barrel-shaped, glaucous; valves enclosed.

Cultivated material is often sold as *Eucalyptus tetragona* (R. Br.) F. Muell., a misapplied name.

4 (2) and 4 (13′). Eucalyptus polyanthemos Schauer in Walp., Repert. Bot. Syst. 2(5): 924. 1843.

Common name: red box or silver dollar gum.

Voucher: U.S.A. California, *Twisselmann 18559* (CAS).

Native to: New South Wales, Victoria.

Trees; bark rough, gray, flaky, and fibrous on the lower trunk or smooth, gray, white, and smooth on upper branches; branchlets occasionally glaucous; crown of mature tree with occasional juvenile and intermediate leaves. Crown leaves alternate, concolorous, ovate to lanceolate, petiolate, dull, blue-green, gray-green, or glaucous. Inflorescences compound, at branch tips. Operculum scar present. At anthesis, flowers white; outer stamens without anthers; stamens shed together in a ring. Fruits urn- or barrel-shaped, glaucous; valves enclosed.

8 (15′). Eucalyptus polybractea F. Muell. ex R. T. Baker, Proc. Linn. Soc. New South Wales 25: 692–693, tab. xlvi, figs. 7–8. 1901.

Common name: blue-leaved mallee.

Voucher: U.S.A. California, *Yost & Ritter 212* (OBI).

Native to: New South Wales, South Australia, Victoria.

Mallees; bark rough, gray, short-fibered, hard; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, dull, bluish gray or bluish green, entire. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, round in cross-section, green; operculum rounded or conical, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cylindrical to barrel-shaped; valves enclosed or near rim level.

4 (15). Eucalyptus populnea F. Muell., J. Proc. Linn. Soc., Bot. 3: 93. 1859 [1858].

Common name: Bimbil box.

Voucher: Australia, *F. M. Reed 3758* (UC).

Native to: New South Wales, Queensland.

Trees; bark rough, gray, short-fibered, hard, rough to the smallest branches; crown of mature tree with occasional intermediate leaves. Crown leaves alternate, concolorous, orbicular to ovate, glossy, green, thick, with long slender petioles. Inflorescences compound, at branch tips. Operculum rounded, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped; valves enclosed or near rim level.

5 (12). Eucalyptus preissiana Schauer in Lehm., Pl. Preiss. 1(1): 131–132. 1844.

Common name: bell-fruited mallee.

Voucher: U.S.A. California, *Ritter 129* (OBI).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark smooth, gray. Leaves alternate or occasionally opposite, concolorous, broadly lanceolate, thick, dull, bluish green. Inflorescences as axillary umbels; peduncles broadly flattened; buds 3 per umbel; operculum rounded and flattened, operculum scar absent, but appearing present due to a color change between the hypanthium and the operculum. At anthesis, flowers yellow. Fruits sessile, bell- to funnel-shaped; valves at rim level.

1 (6). Eucalyptus pruinosa Schauer in Walp., Repert. Bot. Syst. 2(5): 926. 1843.

Common name: silver box or silverleaf box.

Voucher: U.S.A. California, *Ritter 47* (OBI).

Native to: North Australia, Northern Queensland, North West Australia.

Mallees, occasionally small trees; bark rough, gray, flaky, hard, rough to the smallest branches; branchlets glaucous, square in cross-section, pith lacking oil glands; crown of mature tree composed of juvenile leaves. Crown leaves opposite, sessile, concolorous, entire, not fused, ovate to elliptical, glaucous, wrapping around the stem at the base. Inflorescences compound, at branch tips. Operculum conical, operculum scar present. At anthesis, flowers cream-colored; all stamens with anthers. Fruits cylindrical; valves near rim level or slightly exserted.

5 (23′). Eucalyptus pseudoglobulus Naudin ex Maiden, Crit. Rev. Eucalyptus 8: 28. 1929.

Common name: Victorian eurabbie.

Voucher: U.S.A. California, *E. F. Constable 7403* (UC).

Native to: Victoria.

Trees; bark smooth, usually with imperfectly shed rough bark on the basal area of trunk. Leaves alternate, concolorous, lanceolate and sickle-shaped, dark green. Inflorescences axillary umbels; peduncle stout; buds 3 per umbel, stoutly pedicellate, glaucous or not; operculum warty, flattened, with a central knob, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits shortly pedicellate or sessile, funnel- to bell-shaped; valves at rim level or slightly exserted.

8 (24). Eucalyptus pterocarpa C. A. Gardner ex P. J. Lang, Fl. Australia 19: 510. 1988.

Common name: Norseman gum.

Voucher: Western Australia, 8.7 km W on rd. 10.9 km NW of Norseman, *G. M. Chippendale 154* (type, CANB, not seen).

Native to: South West Australia.

Small trees; lacking a lignotuber; bark smooth, pinkish gray or white; branchlet pith glandular. Leaves alternate, concolorous, lanceolate to narrowly lanceolate, glossy. Inflorescences axillary umbels; peduncles slender; buds 7 per umbel, pedicellate, conspicuously ribbed, green; operculum beaked or conical, operculum scar present; stamens inflexed in bud (bent downward under operculum). At anthesis, flowers white. Fruits funnel-shaped with prominent ribs; valves at rim level or slightly exserted.

6 (19). Eucalyptus pulchella Desf., Tabl. École Bot. 284, 408. 1829.

Common name: white peppermint.

Voucher: U.S.A. California, *Kawahara 800* (CAS).

Native to: Tasmania. Naturalized: California, New Zealand.

Trees; bark smooth. Leaves alternate, concolorous, narrowly lanceolate, smelling of peppermint when crushed; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 11, 15 or more per umbel, smooth, green; operculum rounded, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, on pedicels < 0.5 cm long; valves at rim level or enclosed.

1 (12). Eucalyptus pulverulenta Sims, Bot. Mag. 46: pl. 2087. 1819.

Common name: silver-leaved mountain gum.

Voucher: U.S.A. California, *Ritter 18* (OBI).

Native to: New South Wales.

Mallees or shrubs; bark smooth, shedding in ribbons; branchlets glaucous, round in cross-section; crown of mature tree composed primarily of juvenile leaves. Crown leaves opposite, concolorous, sessile, orbicular or heart-shaped, wrapping around the stem, not fused. Inflorescences axillary umbels; buds 3 more per umbel, sessile, glaucous; operculum smooth, conical, beaked, operculum scar present. At anthesis, flowers white. Fruits sessile, cup-shaped, glaucous, < 1.5 cm wide; valves exserted or near rim level.

3 (10). Eucalyptus punctata DC., Prodr. 3: 217. 1828.

Common name: gray gum.

Voucher: U.S.A. California, *Yost & Ritter 264* (OBI).

Native to: New South Wales.

Trees; bark smooth, gray, pink, brown, orange, granular. Leaves alternate, discolorous, broadly lanceolate. Inflorescences axillary umbels; peduncle flattened; buds 7 per umbel, green; operculum conical, operculum scar present. At anthesis, flowers white. Fruits hemispherical to cup-shaped; valves exserted.

1 (12′) and 5 (18). Eucalyptus pyriformis Turcz., Bull. Soc. Imp. Naturalistes Moscou 22(2): 22. 1849.

Common name: Dowerin rose.

Voucher: Australia, 1909, *J. H. Maiden s.n.* (UC1327342).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark smooth; branchlets glaucous, pith without oil glands. Leaves alternate, concolorous, lanceolate, dull. Inflorescences axillary umbels; peduncles stout; buds 3 per umbel, pedicellate, distinctly ribbed; operculum conical to rounded, ribbed, operculum scar present. At anthesis, flowers red, pink, or yellow. Fruits hemispherical to funnel-shaped, occasionally glaucous, > 2 cm wide; disk of fruit raised; valves at rim level.

6 (20′). Eucalyptus racemosa Cav., Icon. 4: 24. 1797.

Common name: scribbly gum.

Voucher: Australia, *L. A. S. Johnson 40158* (UC).

Native to: New South Wales, Southern Queensland.

Trees; bark smooth, with prominent scribbles in the wild, but not usually in cultivation; branchlets smooth, green or brown, not glaucous. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 9 to 15 per umbel, round in cross-section; operculum conical, operculum scar absent. At anthesis, flowers white; some outer stamens without anthers. Fruits hemispherical, shortly pedicellate, to 0.6 cm wide and 0.7 cm long; valves near rim level.

6 (12′). Eucalyptus radiata Sieber ex DC., Prodr. 3: 218. 1828.

Common name: narrow-leaved peppermint.

Voucher: U.S.A. California, 1896, *J. H. Barber s.n.* (UC-40999).

Native to: New South Wales, Southern Queensland, Victoria.

Trees; bark rough, gray-brown, finely fibrous. Juvenile leaves opposite, sessile, narrowly lanceolate or linear, green; adult leaves alternate, concolorous, lanceolate to sickle-shaped, > 1 cm wide; leaf side veins angling toward leaf margin, not parallel-veined; leaf bases tapering evenly, or almost evenly, to the petiole. Inflorescences as axillary umbels; buds 11, 15 or more per umbel; operculum rounded, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped; valves at rim level.

6 (4′). Eucalyptus regnans F. Muell., Annual Rep. Acclim. Soc. Victoria, 20. 1870.

Common name: mountain ash.

Voucher: U.S.A. California, 1907, *H. B. Williamson s.n.* (UC607007).

Native to: Tasmania, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark smooth, rough only on lower trunk, gray-brown, fibrous, then smooth gray or white on upper trunk and larger limbs. Leaves alternate, concolorous, lanceolate to sickle-shaped; leaf side veins angling toward leaf margin, sometimes parallel; leaf bases tapering to petiole unevenly (oblique), or occasionally tapering evenly to the petiole. Inflorescences paired umbels in leaf axils; buds 11 to 15, or more per umbel; operculum conical, beaked, operculum scar absent. Flowers white; all stamens with anthers. Fruits cup-shaped; valves at rim level or enclosed.

3 (20′). Eucalyptus resinifera Sm. in J. White, J. Voy. New South Wales, 231. 1790.

Common name: red mahogany.

Voucher: U.S.A. California, *Yost & Ritter 262* (OBI).

Native to: New South Wales, Queensland. Naturalized: Hawaii, New Zealand.

Trees; bark rough, thick, fibrous, reddish brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences axillary umbels; peduncles flattened; buds 7 or more per umbel; operculum conical, slightly beaked, or horn-shaped, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, hemispherical, 1 cm or less wide; disk of fruit ascending; valves strongly exserted, tips free at maturity.

1 (11). Eucalyptus rhodantha Blakely & H. Steedman, Proc. Linn. Soc. New South Wales, ser. 2, 63: 68. 1938.

Common name: rose mallee.

Voucher: Western Australia, Victoria Plains, near Gunyidi, Dec. 1934, *H. Steedman s.n.* (type, NSW, not seen).

Native to: South West Australia.

Mallees or shrubs; bark smooth, shedding in ribbons; branchlets glaucous, round in cross-section; crown of mature tree composed primarily of juvenile leaves. Crown leaves opposite, concolorous, sessile, orbicular or heart-shaped, wrapping around the stem, not fused. Inflorescences solitary, glaucous flowers in leaf axils; peduncle downturned; buds pedicellate, spherical, glaucous; operculum smooth, beaked, operculum scar present. At anthesis, flowers red. Fruits pedicellate, saucer- to funnel-shaped; valves exserted.

1 (2′). Eucalyptus risdonii Hook. f., London J. Bot. 6: 477. 1847.

Common name: Risdon peppermint.

Voucher: U.S.A. California, 1912, *F. Walter s.n.* (UC-170366).

Native to: Tasmania.

Trees; bark smooth, gray, white, shedding in ribbons; branchlets glaucous; crown of mature trees mostly composed of juvenile leaves. Juvenile leaves opposite, glaucous, fused at the bases, forming a ring; adult leaves alternate, concolorous, petiolate, ovate to broadly lanceolate, glaucous. Inflorescences axillary umbels; buds 9 to 15 per umbel, round in cross-section, glaucous, pedicellate; operculum smooth, rounded, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, hemispherical or cup-shaped, glaucous or not; valves enclosed.

3 (18). Eucalyptus robusta Sm., Spec. Bot. New Holland, Pt. 4: 39, pl. 13. 1795.

Common name: swamp mahogany.

Voucher: U.S.A. California, *Pollard s.n.* (CAS-556588).

Native to: New South Wales, Southern Queensland. Naturalized: Brazil, California, Florida, Hawaii, Mediterranean Basin, New Zealand, South Africa, Sri Lanka, Zimbabwe.

Trees; bark rough, thick, fibrous, reddish brown. Leaves alternate, discolorous, broadly lanceolate. Inflorescences axillary umbels; peduncles flattened; buds 9 to 15 per umbel, cream-colored; operculum conical and beaked, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cylindrical to barrel-shaped; valves of the mature fruit fused across the fruit opening.

8 (3′). Eucalyptus roycei S. G. M. Carr, D. J. Carr & A. S. George, Proc. Roy. Soc. Victoria 83: 159. 1970.

Common name: Shark Bay mallee.

Voucher: Western Australia, near Hamelin Pool, 32.5 mi. [52.3 km] along Loop Rd., 64 mi. [103 km] W of Overlander Rd. House, Great Northern Hwy., 2 Mar. 1966, *E. M. Scrymgeour & S. G. M. Carr 284* (type, PERTH).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark rough, fibrous, and flaky on lower trunk smooth, greenish brown above; branchlet pith glandular. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 or 9 per umbel, square in cross-section. At anthesis, flowers pale yellow; all stamens with anthers. Fruits cylindrical, barrel-shaped, square in cross-section or 4-angled; valves enclosed.

5 (25). Eucalyptus rubida H. Deane & Maiden, Proc. Linn. Soc. New South Wales 24: 456–458, pl. 40. 1899.

Common name: blackbutt candlebark.

Voucher: U.S.A. California, *Yost & Ritter 181* (OBI).

Native to: New South Wales, Tasmania, Victoria.

Trees; bark smooth, white, powdery, with some imperfectly shed rough bark on the basal area of trunk, shedding in ribbons from smaller branches. Leaves alternate, concolorous, lanceolate to sickle-shaped. Inflorescences axillary umbels; buds 3 per umbel, glaucous or not, round in cross-section; operculum smooth, conical and beaked, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, hemispherical, glaucous, disk of fruit raised; valves exserted.

9 (14′). Eucalyptus rudis Endl., Enum. Pl. 49. 1837.

Common name: flooded gum.

Voucher: U.S.A. California, *Yost & Ritter 203* (OBI).

Native to: South West Australia. Naturalized: Hawaii.

Trees; bark rough, gray, fibrous, compacted, flaky to the smallest branches or occasionally smooth on the smaller branches, not shedding in ribbons. Leaves alternate, concolorous, lanceolate to ovate. Inflorescences axillary umbels; buds 7 per umbel; operculum conical or rounded, operculum scar present. At anthesis, flowers white. Fruits pedicellate, hemispherical to cup-shaped; disk of fruit broad, level; valves exserted.

3 (11′). Eucalyptus saligna Sm., Trans. Linn. Soc. London 3: 285. 1797.

Common name: Sydney blue gum.

Voucher: U.S.A. California, *H. H. Smith 4497* (UC).

Native to: New South Wales, Southern Queensland. Naturalized: Florida, Hawaii, New Zealand, South Africa, Sri Lanka, South West Australia.

Trees; bark smooth, white, powdery, with a 1–4 m stocking of flaky, gray, rough bark at the base. Leaves alternate, discolorous, lanceolate. Inflorescences axillary umbels; peduncle flattened; buds 7, 9, or 11 per umbel, not glaucous; operculum conical to beaked, operculum scar present. At anthesis, flowers

white. Fruits funnel-shaped; valves usually 4, exserted and erect, not incurved.

9 (17). Eucalyptus salmonophloia F. Muell., Fragm. 11(88): 11–12. 1878.

Common name: salmon gum.

Voucher: Australia, *H. M. Hall 75* (UC-177948).

Native to: South West Australia.

Trees; bark smooth, white, gray, coppery, salmon-pink, or orange, shiny; branchlet pith without oil glands; branchlets not glaucous. Leaves alternate, concolorous, linear to narrowly lanceolate, glossy. Inflorescences axillary umbels; buds 7 or more per umbel; operculum rounded, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves thin, needle-like, exserted.

9 (16′). Eucalyptus salubris F. Muell., Fragm. 10(83): 54. 1876.

Common name: gimlet.

Voucher: Australia, 1909, *J. H. Maiden s.n.* (UC-447035).

Native to: South West Australia. Naturalized: Queensland, South Africa.

Small trees or shrubs, lacking a lignotuber; bark smooth, tan or coppery, shiny; branchlet pith glandular; branchlets not glaucous. Leaves alternate, concolorous, lanceolate to narrowly lanceolate, glossy. Inflorescences axillary umbels; buds 7 per umbel; operculum rounded, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

9 (19′). Eucalyptus scoparia Maiden, Proc. Linn. Soc. New South Wales, 29: 777–778. 1905.

Common name: Wallangara white gum.

Voucher: Australia, *E. F. Constable NSW 56603* (UC).

Native to: New South Wales, Southern Queensland.

Trees; bark smooth, powdery to the touch, white, gray, mottled; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, narrowly lanceolate, sickle-shaped, glossy, green. Inflorescences axillary umbels; buds 7 per umbel; operculum conical to beaked, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

5 (15′). Eucalyptus serraensis P. Y. Ladiges & T. Whiffin, Austral. Syst. Bot. 6(4): 367. 1993.

Common name: Grampians stringybark.

Voucher: Australia, Grampians, Vic., just N of carpark at Sundial Turntable, on a rocky outcrop, 30 Apr. 1987, *M. R. Newnham & P. Y. Ladiges 943* (type, MEL).

Native to: Victoria.

Mallees or occasionally trees; bark rough, fibrous, hard; young branches warty, glaucous. Leaves alternate, concolorous, lanceolate to ovate, glossy, thick. Inflorescences axillary umbels; buds 3 per umbel, wrinkled and warty; operculum rounded, warty, operculum scar absent. At anthesis, flowers white. Fruits hemispherical, sessile; valves exserted.

2 (7′). Eucalyptus siderophloia Benth., Fl. Austral. 3: 220. 1866 [1867].

Common name: ironbark.

Voucher: U.S.A. California, 1908, *N. S. Ingham s.n.* (UC-1552463).

Native to: New South Wales, Queensland.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs. Leaves alternate, concolorous, lanceolate. Inflorescences compound, at branch tips; buds with operculum conical, equal in length to the hypanthium, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup- or barrel-shaped, 0.5–0.7 cm wide; valves slightly exserted or at rim level.

2 (4). Eucalyptus sideroxylon A. Cunn. ex Woolls., Proc. Linn. Soc. New South Wales, ser. 2, 1(3): 859–860. 1886.

Common name: red ironbark.

Voucher: U.S.A. California, *McClintock s.n.* (CAS-863986).

Native to: New South Wales, Southern Queensland, Victoria. Naturalized: California, Hawaii, Mediterranean Basin, New Zealand, South Africa.

Trees; bark rough, ironbark type, deeply furrowed, hard, dark brown, gray, or black, retained on trunk and limbs. Leaves alternate, concolorous, lanceolate, dull, bluish green, occasionally glaucous. Inflorescences axillary umbels; buds 7 per umbel, ovoid, on slender pedicels; operculum conical to beaked, operculum scar absent. At anthesis, flowers white, pink, or red; outer stamens without anthers. Fruits cup-shaped; valves enclosed.

2 (4′) and 6 (8). Eucalyptus sieberi L. A. S. Johnson, Contr. New South Wales Natl. Herb. 3: 125. 1962.

Common name: silvertop ash.

Voucher: U.S.A. California, *H. H. Smith 4510* (UC).

Native to: New South Wales, Tasmania, Victoria. Naturalized: New Zealand, South Africa.

Trees; bark rough, gray-brown, furrowed, hard, retained on trunk and larger limbs. Leaves alternate, concolorous, lanceolate, glossy; leaf side veins angling toward leaf margin, not parallel-veined. Inflorescences axillary umbels; buds 7 to 15 per umbel; operculum rounded and flattened, operculum scar absent. At anthesis, flowers white; outer stamen without anthers. Fruits barrel-shaped; valves at rim level or enclosed.

9 (10′). Eucalyptus smithii R. T. Baker, Proc. Linn. Soc. New South Wales 24: 292–294, tab. 20. 1899.

Common name: blackbutt peppermint.

Voucher: Australia, 1924, *W. A. W. de Beugerville s.n.* (UC-283216).

Native to: New South Wales, Victoria.

Trees; bark rough, compact, brown or gray, shed as ribbons from the upper limbs; branches not glaucous. Leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 per umbel, diamond-shaped, green; operculum conical to beaked, operculum scar present. At anthesis, flowers white. Fruits pedicellate, cup-shaped; disk of fruit prominent, clearly ascending; valves exserted.

8 (23). Eucalyptus spathulata Hook., Hooker's Icon. Pl. 7: tab. 611. 1844.

Common name: swamp mallet.

Voucher: U.S.A. California, *Yost & Ritter 365* (OBI).

Native to: South West Australia.

Trees; bark smooth, shiny, satiny, coppery, bronze to steely gray; branchlet pith glandular. Leaves alternate, concolorous, linear, glossy. Inflorescences axillary umbels; buds 7 per umbel; operculum horn-shaped, all stamens erect when in bud (not bent under operculum), operculum scar present. At anthesis, flowers white. Fruits cup-shaped; valves at rim level.

5 (21). Eucalyptus steedmanii C. A. Gardner, J. Roy. Soc. Western Australia 19: 87. 1933.

Common name: Steedman's mallet.

Voucher: Western Australia, Forrestania, S of Southern Cross, Feb. 1928, *H. Steedman s.n.* (type, PERTH).

Native to: South West Australia.

Trees; bark smooth, satiny, bronze, pink, and gray; branchlet pith glandular. Leaves alternate, concolorous, elliptical to lanceolate, glossy. Inflorescences axillary umbels; buds 3 per umbel; pedicellate, square in cross-section, winged; operculum conical. At anthesis, flowers white; all stamens with anthers. Fruits funnel-shaped, square in cross-section, winged; valves at rim level or exserted.

6 (6′). Eucalyptus stellulata Sieber ex DC., Prodr. 3: 217. 1828.

Common name: black sally.

Voucher: U.S.A. California, *C. T. White 11491* (UC).

Native to: New South Wales, Victoria.

Trees; bark rough, gray-brown, on lower part of the trunk. Leaves alternate, concolorous, lanceolate; leaf side veins nearly parallel and prominently 3-veined. Inflorescences axillary umbels; buds 9 to 15 per umbel, spindle-shaped and in starlike clusters; operculum conical, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped to globose; valves at rim level or enclosed.

5 (3). Eucalyptus stoatei C. A. Gardner, J. Roy. Soc. Western Australia 22: 126. 1936.

Common name: scarlet pear gum.

Voucher: Western Australia, Bandalup Creek near Kundip, June 1935, *K. F. Dureau & J. E. Harrison s.n.* (type, PERTH).

Native to: South West Australia.

Small trees or shrubs, lacking a lignotuber; bark smooth, pale gray, shedding in strips; branchlet pith without oil glands. Leaves alternate, concolorous, elliptic to lanceolate, glossy. Inflorescences solitary flowers in leaf axils; peduncles slender; buds bright red, round in cross-section, pear-shaped with many ribs, pedicellate; operculum conical, operculum scar present. At anthesis, flowers yellow. Fruits barrel-shaped, ribbed; valves enclosed.

7 (12). Eucalyptus stricklandii Maiden, J. Nat. Hist. Sci. Soc. Western Australia 3(2): 175. 1911.

Common name: Strickland's gum.

Voucher: U.S.A. California, *Yost & Ritter 325* (OBI).

Native to: South West Australia.

Trees; bark rough, flaky, gray, brown, and black on the lower part of the trunk, smooth on upper trunk and limbs; branches often steeping ascending; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, glossy, thick. Inflorescences axillary

umbels; peduncles broad, flattened, glaucous; buds 7 per umbel, sessile, not glaucous; operculum rounded and conical, operculum scar present. At anthesis, flowers white. Fruits sessile, funnel-shaped to bell-shaped; valves at rim level or slightly exserted.

7 (7). Eucalyptus talyuberlup D. J. Carr & S. G. M. Carr, Austral. J. Bot. 28(5–6): 543, figs. 6e, 36. 1980.

Common name: pretty yate.

Voucher: Australia, Western Australia, Stirling Range Nat. Park, Stirling Range Drive, 10 Aug. 1974, *D. J. Carr & S. G. M. Carr 1974* (type, PERTH).

Native to: South West Australia.

Trees or mallees; lignotuber present; bark smooth, pale gray; branchlet pith without oil glands. Leaves alternate, concolorous, narrowly lanceolate, glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 7 or more per umbel, free at the base, green; operculum smooth or slightly warty, operculum scar present. At anthesis, flowers yellow to chartreuse. Fruits sessile, free at the base, funnel- to bell-shaped, valves exserted, tips connected at maturity.

9 (22′). Eucalyptus tereticornis Sm., Spec. Bot. New Holland, Pt. 4: 41–42. 1795.

Common name: forest red gum.

Voucher: U.S.A. California, *Boyd s.n.* (CAS-931360).

Native to: New South Wales, Queensland, Victoria. Naturalized: California, Hawaii, India, Mediterranean Basin, New Zealand, South Africa, Zimbabwe.

Trees; bark smooth, not powdery to the touch, usually with some imperfectly shed, rough gray bark on the basal area of trunk; branches often steeply ascending; branchlet pith without oil glands. Juvenile leaves opposite for fewer than 5 pairs; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 7 per umbel; operculum horn-shaped or conical, not beaked, 2× longer than hypanthium, operculum scar present. At anthesis, flowers white. Fruits hemispherical; valves exserted.

5 (4). Eucalyptus tetraptera Turcz., Bull. Soc. Imp. Naturalistes Moscou 22(2): 22. 1849.

Common name: square-fruited mallee.

Voucher: U.S.A. California, *P. Ashley s.n.* (OBI-52779).

Native to: South West Australia.

Mallees or shrubs; lignotuber present; bark smooth, pale gray, sometimes with persistent ribbons on the branches; branchlets square in cross-section, pith without oil glands. Leaves alternate, concolorous, broadly lanceolate, thick, glossy. Inflorescences solitary flowers in leaf axils; peduncles flat, stout, downturned; buds bright red, square in cross-section, with 4 wings, sessile; operculum conical, operculum scar present. At anthesis, flowers red. Fruits square in cross-section, winged, > 2.5 cm wide; valves enclosed.

8 (28). Eucalyptus torquata Luehm., Vict. Naturalist 13: 147. 1897.

Common name: coral gum.

Voucher: U.S.A. California, *Keil 11872-6* (OBI).

Native to: South West Australia.

Trees; bark rough, scaly, dark, fibrous on lower trunk, smooth above; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, dull, bluish green. Inflorescences axillary umbels; buds 7 per umbel, cylindrical with prominent ribs at the base; operculum beaked with an expanded, ribbed base, operculum scar present. At anthesis, flowers pink; all stamens with anthers. Fruits pedicellate, cylindrical, ribbed; valves enclosed.

1 (14) and 5 (29). Eucalyptus urnigera Hook. f., London J. Bot. 6: 477–478. 1847.

Common name: urn gum.

Voucher: U.S.A. California, *Ritter 83* (OBI).

Native to: Tasmania.

Trees; bark smooth; branchlets glaucous; crown of mature tree composed of juvenile and adult leaves. Juvenile leaves opposite, glaucous, sessile, entire, orbicular, free; adult leaves alternate, concolorous, lanceolate to elliptical, dull, blue-green, glaucous, petiolate, entire. Inflorescences axillary umbels; peduncles as long as or longer than buds, often downturned; buds 3 per umbel, glaucous, round in cross-section; operculum smooth, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits glaucous, urn-shaped, shortly pedicellate; valves enclosed.

3 (9′). Eucalyptus urophylla S. T. Blake, Austrobaileya 1(1): 7. 1977.

Common name: Timor mountain gum.

Voucher: U.S.A. California, *Turnbull 210* (type, FRI, not seen).

Native to: Indonesia, East Timor. Naturalized: Hawaii.

Trees; bark rough, fibrous, scaly, reddish brown on lower trunk, smooth on upper trunk and limbs. Leaves alternate, discolorous, broadly lanceolate.

Inflorescences axillary umbels; peduncle slightly flattened; buds 7 or more per umbel; operculum conical; operculum scar present. At anthesis, flowers white. Fruits cup-shaped; valves at rim level or slightly exserted.

7 (20). Eucalyptus utilis Brooker & Hopper, Nuytsia 14(3): 349, figs. 6, 7. 2002.

Common name: coastal moort.

Voucher: U.S.A. California, *Kelch 06538* (OBI).

Native to: South West Australia.

Small trees or shrubs; bark smooth, gray to coppery; branchlet pith glandular. Leaves alternate, concolorous, lanceolate (usually > 5× longer than wide), glossy. Inflorescences axillary umbels; peduncles broad, flattened, and straplike; buds 7 per umbel, ridged; operculum conical or horn-shaped; all stamens erect when in bud (not bent under operculum), operculum scar present. At anthesis, flowers white or cream-colored. Fruits sessile, barrel- to funnel-shaped; valves at rim level.

This species is often erroneously sold under the name *Eucalyptus platypus* var. *heterophylla* Blakely.

5 (11). Eucalyptus vernicosa Hook. f., London J. Bot. 6: 478. 1847.

Common name: varnished gum.

Voucher: Australia, Mt. Fatigue, Tasmania, 4 Apr. 1842, *R. Gunn 1113* (type, K, not seen).

Native to: Tasmania.

Shrubs; lignotuber present; bark smooth, gray. Leaves alternate, concolorous or slightly discolorous, orbicular to ovate, crowded on the the stem, < 4 cm long. Inflorescences axillary umbels; buds 3, occasionally 1, per umbel; operculum smooth, conical, operculum scar present. At anthesis, flowers white. Fruits hemispherical, sessile; valves near rim level.

5 (26). Eucalyptus viminalis Labill., Nov. Holl. Pl. 2: 12–13, tab. 151. 1806.

Common name: manna gum or ribbon gum.

Voucher: U.S.A. California, *Keil 25866* (OBI).

Native to: New South Wales, South Australia, Tasmania, Victoria. Naturalized: California, Hawaii, New Zealand, South Africa.

Trees; bark smooth, occasionally with short stocking of rough bark; smooth bark white, gray, or cream, shedding in ribbons. Juvenile leaves lanceolate, green, sessile; adult leaves alternate, concolorous, lanceolate. Inflorescences axillary umbels; buds 3 per umbel, round in cross-section, green; operculum conical, smooth, operculum scar present. At anthesis, flowers white; all stamens with anthers. Fruits cup-shaped, not glaucous, disk raised; valves exserted.

8 (15). Eucalyptus viridis R. T. Baker, Proc. Linn. Soc. New South Wales 25: 316–319, pl. 19. 1900.

Common name: green mallee.

Voucher: U.S.A. California, *Yost & Ritter 300* (OBI).

Native to: New South Wales, South Australia, Southern Queensland, Victoria.

Mallees; bark rough, gray, short-fibered, hard; branchlet pith without oil glands. Leaves alternate, concolorous, narrowly lanceolate to linear, green, entire. Inflorescences axillary umbels; buds 7, 9, or 11 per umbel, round in cross-section, green; operculum rounded or conical, operculum scar absent. At anthesis, flowers white; all stamens with anthers. Fruits pedicellate, cup-shaped; valves enclosed or near rim level.

7 (16′). Eucalyptus wandoo Blakely, Key Eucalypts, 112. 1934. Basionym: *Eucalyptus redunca* var. *elata* Benth., Fl. Austral. 3: 253. 1867. Blocking name: *Eucalyptus elata* Dehnh., Cat. Horti Camald. 26. 1829.

Common name: wandoo.

Voucher: U.S.A. California, *Yost & Ritter 355* (OBI).

Native to: South West Australia.

Trees; bark smooth, flaky, mottled, white, pale gray, cream; branchlet pith glandular. Leaves alternate, concolorous, lanceolate, dull, slightly blue-green. Inflorescences axillary umbels; peduncles flattened, green; buds 11 or more per umbel; operculum horn-shaped, operculum scar present. At anthesis, flowers white. Fruits cylindrical to barrel-shaped; valves enclosed or at rim level.

8 (22). Eucalyptus woodwardii Maiden, J. Nat. Hist. Sci. Soc. Western Australia 3(1): 42–43. 1910.

Common name: lemon-flowered gum.

Voucher: U.S.A. California, *Yost & Ritter 368* (OBI).

Native to: South West Australia.

Trees; lignotuber absent; bark smooth, white, shedding in ribbons. Leaves alternate, concolorous, lanceolate, dull, grayish green. Inflorescences axillary umbels; buds 7 per umbel, glaucous, pedicellate; operculum beaked, operculum scar present. At anthesis, flowers yellow. Fruits bell- to funnel-shaped; valves enclosed or at rim level.

5 (17′). Eucalyptus youngiana F. Muell., Fragm. 10(81): 5–6. 1876.

Common name: large-fruited mallee.

Voucher: Western Australia, Queen Victoria Spring, 1875, *J. Young s.n.* (type, MEL).

Native to: South Australia, South West Australia.

Mallees or shrubs; bark rough, fibrous on trunk, smooth, white on smaller branches; branchlet pith without oil glands. Leaves alternate, concolorous, lanceolate, dull, bluish green. Inflorescences axillary umbels; peduncles stout; buds 3 per umbel, distinctly ribbed, pedicellate; operculum conical, beaked, ribbed, operculum scar present. At anthesis, flowers red, pink, or yellow. Fruits disk shaped, > 3 cm wide.

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UPDATED TAXONOMY OF *GAERTNERA* (RUBIACEAE, GAERTNEREAE) IN MADAGASCAR, WITH SIXTEEN NEW SPECIES

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ABSTRACT

Gaertnera Lam. (Rubiaceae, Gaertnereae) includes 42 species confirmed from Madagascar, with 16 of them newly described here as a result of recent botanical exploration. The Madagascar species of *Gaertnera* have notable morphological variation. Newly described, illustrated, and keyed here are *G. arenarioides* C. M. Taylor, *G. breviflora* C. M. Taylor, *G. hirsuta* C. M. Taylor, *G. laevis* C. M. Taylor, *G. littoralis* C. M. Taylor, *G. malcomberiana* C. M. Taylor, *G. masoalana* C. M. Taylor, *G. nitida* C. M. Taylor, *G. rakotovaoana* C. M. Taylor, *G. razakamalalana* C. M. Taylor, *G. robusta* C. M. Taylor, *G. rubra* C. M. Taylor, *G. sclerophylla* C. M. Taylor, *G. velutina* C. M. Taylor, *G. vernicosa* C. M. Taylor, and *G. xerophila* C. M. Taylor. Narrower circumscriptions of *G. obovata* Baker var. *sphaerocarpa* (Baker) Malcomber and *G. phanerophlebia* Baker here are detailed by revised descriptions. Assessments of conservation status of *Gaertnera* in Madagascar using IUCN categories find two species Critically Endangered, 10 Endangered, 14 Vulnerable, two Near Threatened, and 14 species and two varieties of Least Concern.

Key words: *Gaertnera*, Gaertnereae, IUCN Red List, Madagascar, Rubiaceae.

Gaertnera Lam. (Rubiaceae, Gaertnereae) comprises shrubs and small trees found in tropical Africa, Madagascar, the Mascarene Islands, Sri Lanka, and Southeast Asia. The recent revision of *Gaertnera* (Malcomber & Taylor, 2009) recognized 69 species with four varieties plus one putative hybrid. *Gaertnera* can be recognized by its woody habit; opposite or ternate leaves; stipules that are united around the stem into a tubular structure and usually also fused to ridges or wings that encircle the petioles; cymose, bracteate inflorescences with the flowers solitary to numerous in variously a terminal, axillary, and/or pseudoaxillary position; generally cupuliform calyx limbs; salverform to funnelform corollas with four or five valvate lobes; ovaries that are superior in flower; and fleshy drupaceous fruits with usually two, rather thin-walled pyrenes. The secondarily superior position of the ovary is unusual in the Rubiaceae (Robbrecht, 1988), and has caused some confusion about the relationships of this genus. *Gaertnera* is also notable for its varied morphology and reproductive biology. This genus includes both distylous and dioecious species, with all plants of a geographic region apparently similar in breeding system: the species of Africa, Madagascar, the Mascarenes, and Sri Lanka are all distylous while the dioecious species are all found in Southeast Asia (Malcomber, 2002; Macomber & Taylor, 2009). *Gaertnera* presents several unusual morphological features, such as enlarged stipules and flexuous pendulous branches. Several of these unusual characters have been derived in parallel in geographically distinct, relatively rapid species radiations (Malcomber, 2002).

The recent revision of *Gaertnera* (Malcomber & Taylor, 2009) differed from the classifications of previous authors in several aspects, including the postulation of interspecific hybridization and narrower species circumscriptions. In particular Beusekom (1967) treated *G. vaginans* (DC.) Merr. as a widely distributed and morphologically variable species found throughout the range of the genus, with both distylous and dioecious plants, variously sessile and capitate to pedunculate and laxly cymose inflorescences, truncate to deeply lobed calyx limbs, and small to large corolla tubes (2.5–16 mm). In contrast, based on data from both morphology and molecular sequences Malcomber (2000) and Malcomber and Taylor (2009) classified the plants of Beusekom's *G.*

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vaginans in 12 distinct species, each of which is restricted to a single geographic region, has a consistent breeding system, and is less variable morphologically. Sufficient evidence was not found to support the separation of infrageneric taxa. This comprehensive revision of the genus provides a basis for further study, and here we present an updated review of *Gaertnera* in Madagascar. Botanical exploration has newly documented extensive areas in the last decade, discovering additional species and character states in the genus.

Gaertnera in Madagascar

Gaertnera comprises 42 species confirmed to be present in Madagascar, all endemic, including the 16 species newly described here. This is a significant increase from the 29 species reported by Malcomber and Taylor (2009), with three of the species reported there based on historical collections with dubious collection localities. These three species, *G. calycina* Bojer, *G. crassiflora* Bojer, and *G. pendula* Bojer, are not included here. The three are all reliably documented from Mauritius, although *G. calycina* and *G. crassiflora* are now considered extinct.

Floristic study of Madagascar has demonstrated recently that Rubiaceae is the second most species-rich family on this island (Davis & Bridson, 2003; Callmander et al., 2011) after Orchidaceae. Among the Rubiaceae here, *Gaertnera* is one of the largest genera (Davis & Bridson, 2003). The drivers of this Rubiaceae diversity are as yet unknown, but molecular analyses estimated *Gaertnera*'s diversification to be relatively recent in geological terms, within the last 5–5.5 million years ago (mya) (Malcomber, 2002).

Following the vegetation classification of Moat and Smith (2007), most of the species of *Gaertnera* in Madagascar are found in humid forest. This genus is also rather well represented in littoral forest, and *G. nitida* C. M. Taylor ranges into dry forest. [The humid forest category of Moat and Smith corresponds to the combined categories "humid forest (low elevation)," "humid forest (mid altitude)," and "humid forest (lower montane)" of Du Puy and Moat (2003). The littoral forest category of Moat and Smith corresponds to the category "eastern coastal forest" of Du Puy and Moat. The dry forest cateogory of Du Puy and Moat corresponds to the category "seasonally dry forest" of Du Puy and Moat.]

Molecular phylogenetic analysis of *Gaertnera* species spanning the entire geographical range of the genus (Malcomber, 2002; Malcomber & Taylor, 2009) hypothesized that the species in Madagascar belong to two separate lineages: (1) *G. lowryi* Malcomber is hypothesized as sister to a clade of Sri Lankan and Southeast Asian species, albeit with marginal support, and (2) a clade containing all the other sampled species of Madagascar is hypothesized a sister to a clade of Mascarene species. This analysis hypothesized either a single or at least two separate dispersal event(s) of *Gaertnera* from Africa to Madagascar, followed by subsequent independent dispersals of *Gaertnera* to the Mascarenes and the region of Sri Lanka and southeastern Asia. Despite the uncertainty on the origins of the Madagascan species of *Gaertnera*, several features are shared by all of them: a distylous breeding system; inflorescence position terminal on main stems or lateral branches; entire (i.e., non-fenestrate) corolla tubes; and fruits with two hemispherical, smooth pyrenes. Otherwise, the full range of variation documented in the genus is found among the *Gaertnera* species in Madagascar.

Malcomber and Taylor (2009) described in detail the stipule morphology of *Gaertnera*, which is distinctive for the genus and often diagnostic for individual species. In general, the stipules are fused around the stem into a well-developed tube or sheath that is subtruncate to triangular at the top and often has one to four lobes. At the base of the stipule, rounded to flattened ridges or wings extend down at each side to encircle the petioles. This stipule form is unique in the Rubiaceae; *Gaertnera*'s Neotropical sister genus *Pagamea* Aubl. has similar stipule sheaths but lacks the wings that encircle the petioles. These stipule wings are also lacking in a few *Gaertnera* species (e.g., *G. laevis* C. M. Taylor), but are well developed in the early-diverging species of the phylogeny presented in Malcomber and Taylor (2009). Two different characteristic stipule morphological forms are found in *Gaertnera* and both are represented in the species of Madagascar. Stipule form is important for identification of species. Tubular stipules have a sheath that is cylindrical and open at the top in bud, so the leaves push through without breaking the sheath; the sheath may then split tardily as the stems enlarge. Calyptrate stipules are fully fused to form a cap covering the bud, so the expanding young leaves have to split the stipule as they push through it. Stipule form is apparently characteristic for a species, although it may be difficult to discern from study of older stipules on lower nodes. Older stipules of both forms are often fragmented by the expanding stem and general deterioration.

Several of the new species described here include some specimens that were classified by Malcomber and Taylor (2009) in previously described species. The circumscription and description of those previously described species are not appreciably changed

by removal of these specimens, except in two cases: *Gaertnera obovata* Baker var. *sphaerocarpa* (Baker) Malcomber and *G. phanerophlebia* Baker are more narrowly circumscribed here. Revised descriptions of both species are presented. In addition, the conservation status of the *Gaertnera* species and varieties in Madagascar is assessed here, as noted under each individual species and summarized in Table 1.

Methods

The species concept used here is similar to that of Malcomber and Taylor (2009). The measurements are all taken from dried specimens. Morphological terminology here follows that of Malcomber and Taylor (2009), where explanation and illustrations can be found. Our basic morphological terminology follows that of Radford et al. (1974). Stipule morphology is important for identification of *Gaertnera* species, and readers are strongly advised to consult Malcomber and Taylor (2009) for stipule terminology before using the Key to Species presented here. The term "stipule form" refers to the two different stipule morphologies, tubular and calyptrate. The term subsessile here is generally equivalent to a length of 0.3–0.7 mm. The description "opposite" applied here to the leaves denotes an arrangement with two leaves borne at a stem node. The Key to Species below is intended primarily for identification of specimens, rather than as a natural key to the systematic characters of the species. Descriptions and full nomenclature of the previously described species were presented by Malcomber and Taylor (2009) and are not repeated here, except full nomenclature is given for the accepted names cited here and descriptions are presented for the two species with significantly revised circumscriptions. Inflorescence color has not often been noted by collectors, and is not described here due to lack of data. Distributional information presented here is organized first by province (aritany mizakatena), and within each province then by the region (faritra). This organization follows the format of the specimen records in the TROPICOS® database (<http://www.tropicos.org>), and is intended to facilitate retrieval of data there and comparison with older studies. The provinces and regions of Madagascar are detailed on Wikipedia (<http://en.wikipedia.org/wiki/Madagascar#Administrative_divisions>). Vegetation descriptions in the distribution summary of the individual species generally follow those of Moat and Smith (2007), but also incorporate information from collector data regarding local conditions.

The information published here is extensively supplemented by online resources that are continually updated. The TROPICOS® database includes detailed information on *Gaertnera* nomenclature, images of living plants and specimens including types and exemplar specimens, phenology and elevational distribution, and specimen data including distribution maps. The Catalogue of the Vascular Plants of Madagascar (<http://www.tropicos.org/Project/MADA>) includes genus and species pages with a focus on biogeography and floristics of this island and detailed distributional data for each species. The Madagascar Catalogue should be consulted online for distribution maps and data for all the species treated here. The TROPICOS® Rubiaceae Project (<http://www.tropicos.org/Name/40011554projectid=34>) presents genus and species pages for *Gaertnera* with a focus on revisionary information, including morphological descriptions, bibliographic references, keys, and supplemental notes. A vegetation map of Madagascar with information on individual formations is available in The CEPF Madagascar Vegetation Mapping Project (<http://www.vegmad.org/maps.html>).

Conservation status was analyzed by assessing the risk of extinction according to the IUCN Categories and Criteria (IUCN 2012; IUCN Standards and Petitions Working Group 2012), and the methodology of the Catalogue of the Vascular Plants of Madagascar (Callmander et al., 2007). This methodology utilizes primary occurrence data compiled from reliably identified herbarium specimens (i.e., specimens with provisonal determinations were not included) in conjunction with geographical information systems (GIS) software to determine the geographic range size parameters of extent of occurrence (EOO, calculated as the area of the minimum convex polygon containing all points of known, inferred or projected sites of occurrence) and area of occupancy (AOO, estimated on the basis of suitable habitat within the EOO by extrapolating from the minimum area of occupancy as calculated by superimposing a 3.16 × 3.16 km grid onto the primary occurrence points and summing the cumulative area of occupied cells). These area parameters are then compared against threshold values, with the number of locations then determined in the context of threats to the species at known sites of occurrence. The impact of potential threats on continuing and future population decline incorporates two assumptions: (1) ongoing habitat degradation and destruction will leave few significant areas of primary vegetation outside the protected area network; and (2) loss of primary vegetation within protected areas will be minimal. Although some unprotected areas may escape destruction, such as on steep or rugged terrain, it is considered highly

unlikely that populations of long-lived plants will survive outside protected areas for subsequent generations, given Madagascar's high rate of deforestation.

Taxonomy

Gaertnera Lam., Tabl. Encycl. 1: 379, t. 167. 1792, nom. cons. TYPE: *Gaertnera vaginata* Poir.

Gaertnera includes 85 species found from Africa through Madagascar to the Mascarenes, and in Sri Lanka and southeastern Asia. See Malcomber and Taylor (2009: 592, 594–595) for a formal genus description and synonymy. In Madagascar 42 species and two varieties are confirmed present (Table 1).

Key to *Gaertnera* Species and Varieties in Madagascar

1. Stipules persistent as 4 spathulate to linear segments, these often overlapping due to shortened internodes; leaves small, 0.3–1.5 × 0.3–1.8 cm; flowers solitary or 2, sessile or subsessile.
   2. Leaves elliptic; calyx lobes 0.5–2.5 mm long; corolla tube 2.5–3 mm long ..... 10. *G. furcellata* (Baill. ex Vatke) Malcomber & A. P. Davis
   2′. Leaves cuneiform to spathulate or obovate; calyx lobes 2.4–3 mm long; corolla tube 4–4.5 mm long ..... 25. *G. microphylla* Capuron ex Malcomber & A. P. Davis
1′. Stipules variously caducous, deciduous, persistent, or fragmenting, in form spathiform to cylindrical or apparently intra- or interpetiolar, those of successive nodes overlapping to well separated along stem, but not splitting into 4 persistent segments; leaves 0.5–51 × 0.3–14 cm; flowers solitary to numerous, sessile to pedunculate and/or pedicellate.
   3. Young stems and leaves (at least abaxially) hirsute, hispid, pilose, hirtellous, velutinous, and/or tomentulose with spreading trichomes, or strigose to apparently arachnoid-pubescent with appressed trichomes ≥ 1 mm long, or with pubescence forming extensive patches with individual trichomes not evident; flowers 15 or more.
      4. Pubescence of underside of leaf (i.e., abaxial surface) appressed, variously strigose to strigillose and/or lanose or apparently arachnoid.
         5. Leaves elliptic-oblong, 2–7 cm wide, abaxially with pubescence strigose and sometimes also strigillose, with individual trichomes mostly evident; peduncle 0–4 cm long; inflorescence rather laxly cymose ..... 15. *G. ianthina* Malcomber
         5′. Leaves obovate or oblanceolate, 4–8.8 cm wide, abaxially with pubescence lanose or apparently arachnoid at least on costa, with individual trichomes mostly not evident; peduncle 0–0.8 cm long; inflorescence congested cymose ..... 23. *G. malcomberiana* C. M. Taylor
      4′. Pubescence of underside of leaf spreading, variously hirtellous, tomentellous, velutinous, pilose, hispid, and/or hirsute.
         6. Calyx limb lobed, with lobes narrowly lanceolate to elliptic or ovate, 5–13 mm long; leaves with 9 to 12 pairs of secondary veins ..... 31. *G. phyllosepala* Baker
         6′. Calyx limb truncate, denticulate, or lobed, with lobes narrowly triangular to linear, 0.1–14 mm long; leaves with 5 to 30 pairs of secondary veins.
            7. Calyx lobes 1.5–6 mm long with at least some lobes > 3 mm long; bracteoles 3–9 mm long.
               8. Leaves with 14 to 30 pairs of secondary veins, with the intersecondary and higher-order venation regularly evident; inflorescences congested to rather laxly cymose, with secondary axes developed ..... 12. *G. hirsuta* C. M. Taylor
               8′. Leaves with 6 to 14 pairs of secondary veins, with the intersecondary and higher-order venation mostly not visible; inflorescences subcapitate, with secondary axes not or hardly developed ..... 30. *G. phanerophlebia*
            7′. Calyx limb truncate or lobed, with lobes ≤ 3 mm long; bracteoles 0.5–7 mm long.
               9. Plants drying with orange or brownish orange color; stipule tubes 22–68 mm long; corolla tube 10–13 mm long ..... 38. *G. schatzii* Malcomber
               9′. Plants drying with green, grayish green, brownish green, brown, reddish brown, chestnut brown, or orangish brown; stipule tubes 6–35 mm long; corolla tube 4–11 mm long.
                  10. Stems hispid with spreading long trichomes ..... 13. *G. hispida* Aug. D.C.
                  10′. Stems tomentellous, pilosulous, or hirtellous with spreading but rather short trichomes.
                     11. Calyx limb lobed, with lobes 1.5–3 mm long ..... 40. *G. velutina* C. M. Taylor
                     11′. Calyx limb subtruncate to shallowly lobed, with lobes ≤ 1 mm long and at least some shorter than this.
                        12. Leaves obovate or oblanceolate; bracteoles 1–2 mm long; flowers all sessile or mixed sessile and pedicellate, with pedicels 0.5–2 mm long; anthers 1.8–2.2 mm long ..... 28b. *G. obovata* var. *sphaerocarpa*
                        12′. Leaves elliptic-oblong; bracteoles 2–5 mm long; flowers mixed sessile and pedicellate, with pedicels 2–5 mm long; anthers 2–3 mm long ..... 33. *G. rakotovaoana* C. M. Taylor

3′. Young stems and leaves glabrous or puberulous to strigillose or hirtellous, with the pubescence not evident or patchy to sparse with individual trichomes separated or restricted to the principal veins, and flowers 1 to numerous; or, stems pilosulous to strigose, hirtellous, or villosulous, leaves puberulous to glabrous abaxially, and flowers 1 to 5.
13. Flowers solitary or 2 to 5, with inflorescences fasciculate to shortly cymose; leaves 0.5–7 × 0.3–4.2 cm.
14. Youngest internodes longitudinally ridged; leaves 0.5–3.8 × 0.3–2 cm.
15. Flowers borne on pedicels or peduncles 2.5–19 mm long; corolla tube 4–7.5 mm long.
16. Calyx lobes 0.4–4 mm long; stems often 2-winged and with corky bark . . . . . 1. *G. alata* Bremek. ex Malcomber & A. P. Davis
16′. Calyx limb truncate or with lobes ≤ 0.4 mm long; stems with rounded corners, not becoming corky . . . . . 29. *G. pauciflora* Malcomber & A. P. Davis
15′. Flowers sessile or subsessile, with pedicel or peduncle to 1 mm long; corolla tube 2.5–5.5 mm long.
17. Stipules caducous; leaves 0.4–2 cm wide; calyx lobes 1.1–4.2 mm long . . . . . 6. *G. brevipedicellata* Malcomber & A. P. Davis
17′. Stipules persistent or tardily falling via fragmentation; leaves 0.3–0.5 cm wide; calyx lobes 0.5–2.5 mm long . . . . . 10. *G. furcellata*
14′. Youngest internodes smooth; leaves 0.5–7 × 0.3–3.2 cm.
18. Calyx limb truncate or with lobes to 0.4 mm long; stems glabrous.
19. Stipules tubular; inflorescences sessile or with peduncles 9–30 mm long . . . . . 4. *G. bambusifolia* Malcomber & A. P. Davis
19′. Stipules calyptrate; inflorescences with peduncles 2.5–9.1 mm long . . . . 29. *G. pauciflora*
18′. Calyx limb with lobes 0.4–4 mm long; stems glabrous, pilosulous, strigillose, or villosulous.
20. Stems glabrous; leaves 4–6.5 cm long . . . . . 8. *G. darcyana* Malcomber & A. P. Davis
20′. Stems strigillose, pilosulous, or villosulous; leaves 0.5–4 cm long . . . . . 22. *G. madagascariensis* (Hook. f.) Malcomber & A. P. Davis
13′. Flowers several to numerous (6 to 150), with inflorescences subcapitate, congested cymose, laxly cymose, or paniculiform; leaves 3–51 × 1.5–15 cm.
21. Calyx lobed with lobes 0.5–15 mm long, with at least several lobes on most flowers > 1.5 mm long.
22. Calyx lobes regularly to irregularly developed with the largest lobes 5–15 mm long, with at least some lobes narrowly lanceolate, elliptic, elliptic-oblong, or ovate (i.e., narrowed at the base), flowers mostly or all subtended by bracteoles 5–16 mm long, these often white and petaloid.
23. Stipules tubular; bracteoles 5–10 mm long; calyx lobes 5–13 mm long . . . 31. *G. phyllosepala*
23′. Stipules calyptrate; bracteoles 8–16 mm long; calyx lobes 6–15 mm long . . . . . 32. *G. phyllostachya* Baker
22′. Calyx lobes regularly to irregularly developed with the largest lobes 1.5–7 mm long, narrowly to broadly triangular, ligulate, or linear (i.e., mostly not narrowed at base); flowers subtended by bracteoles 0.5–9 mm long, these green to white, generally not petaloid.
24. Flowers 2 to 9 in lax fascicles or cymes; inflorescences with branched portion 0.8–2 × 0.4–2.5 cm . . . . . 8. *G. darcyana*
24′. Flowers 10 or more in congested to lax cymes; inflorescences with branched portion 1–19 × 1–20 cm.
25. Inflorescences subcapitate or congested cymose, subsessile, subglobose, with secondary axes not or hardly developed; stipules calyptrate . . . 30. *G. phanerophlebia*
25′. Inflorescences cymose, branched in 2 to 5 orders, pedunculate or sometimes sessile and apparently 3-partite, corymbiform to pyramidal, with secondary axes developed; stipules calyptrate or tubular.
26. Stipules calyptrate, drying membranceous or papery.
27. Calyx with lobes 3 to 5, ligulate, 1.5–5 mm long in flower (unknown in fruit); corolla tube 3.5–5 mm long; plants drying orangish brown or brown . . . . . 24. *G. masoalana* C. M. Taylor
27′. Calyx wth lobes 1 to 3, triangular to lanceolate or ligulate, 1–3 mm long in flower and up to 5 mm long in fruit; corolla tube 6.5–10 mm long; plants drying greenish brown . . . . . 34. *G. raphaelii* Malcomber
26. Stipules tubular, drying papery to chartaceous.
28. Calyx lobes spathulate and well developed, at least some of them 3.5–7 mm long; leaf venation mostly not evident abaxially; stipules with tube 3–10 mm long . . . . . 14. *G. humblotii* Drake
28′. Calyx lobes triangular to ovate, 0.5–3.5 mm long; leaves with secondary and sometimes higher-order venation evident abaxially; stipules with tube 6–33 mm long.
29. Stipules with tube inflated or funnelform, 10–33 mm long, usually covering most or all of the internode above, at top irregular to broadly 4-lobed, with margins thinly marcescent; petioles 18–20 mm long . . . . . 21. *G. macrostipula* Baker

29′. Stipules with tube cylindrical, 6–16 mm long, covering half or less of the internode above, at top subtruncate and with 4 distinct lobes, with margins not marcescent; petioles 4–15 mm long.
30. Leaves matte on both surfaces; corolla lobes abaxially smooth or only a little thickened ..... 40. *G. velutina*
30′. Leaves often shiny on both surfaces; corolla lobes with well-developed abaxial thickenings or horns ..... 41. *G. vernicosa* C. M. Taylor

21′. Calyx truncate or with lobes up to 1.2 mm long, or occasionally with 1 or 2 lobes on a few flowers up to 2 mm long but in this case at least some of the others < 1.2 mm long.
31. Stipules calyptrate.
32. Bracts 4–50 mm long, lanceolate, elliptic, ligulate, or ovate (i.e., generally narrowed at base); bracteoles 1–16 mm long with at least some of them > 5 mm long.
33. Petioles without stipular wings; bracteoles 1–5 mm long ..... 17. *G. laevis*
33′. Petioles encircled by stipular wings; bracteoles 8–16 mm long ..... 32. *G. phyllostachya*
32′. Bracts 0.8–27 mm long, triangular, ligulate, deltate, lanceolate, narrowly elliptic, or linear (i.e., usually not narrowed at base); bracteoles 0.5–5 mm long.
34. Leaves drying chartaceous to coriaceous, with secondary veins plane to prominulous below or sometimes not evident, with remaining venation plane.
35. Leaves drying subcoriaceous to coriaceous, with secondary veins not visible abaxially; calyx with tube 1.5–2.2 mm long and lobed, with lobes 0.2–1.2 mm long; corolla tube ca. 2.5 mm long ..... 42. *G. xerophila* C. M. Taylor
35′. Leaves drying chartaceous to subcoriaceous, with secondary veins at least weakly visible abaxially; calyx with tube 0.8–1.5 mm long and truncate or lobed, with lobes ≤ 0.4 mm long; corolla tube 3–6 mm long.
36. Leaves elliptic, elliptic-oblong, or oblanceolate, 1.7–13.2 × 0.7–4.6 cm, at base gradually narrowed then cuneate to obtuse; stipules generally caducous; drupes 4.5–5.5 mm in diameter ..... 11. *G. guillotii* Hochr.
36′. Leaves obovate, oblanceolate, or oblong-obovate, 6.5–26 × 3–11 cm, at base somewhat narrowed then rather abruptly obtuse to rounded; stipules deciduous or with basal portion persistent; drupes 7–10 mm in diameter ..... 39. *G. sclerophylla* C. M. Taylor
34′. Leaves drying papery to subcoriaceous, with secondary venation prominulous to prominent below and generally evident, with remaining venation evident or not.
37. Calyx with tube 2–3 mm long and on at least some flowers > 2 mm long; corolla with tube 9–12 mm long.
38. Corolla white; inflorescences with peduncle 9–14 cm long and branched portion 12–22 × 6–22 cm; branchlets 3.5–6 mm diam.; petioles 7–12 mm long; Antsiranana ..... 3. *G. arenarioides* C. M. Taylor
38′. Corolla white, red, pink, orange, or violet; inflorescences sessile or with peduncle to 10.5 cm long and branched portion 3.5–10 × 5–14 cm; branchlets 5–10 mm diam.; petioles 10–40 mm long; Toamasina ..... 37. *G. rubra* C. M. Taylor
37′. Calyx with tube 0.8–2 mm long and on at least some flowers < 2 mm long; corolla with tube 4–9 mm long.
39. Bracteoles generally small, 1–2 mm long ..... 28. *G. obovata* Baker
40. Leaves elliptic, elliptic-oblong, oblanceolate, obovate, or ovate, 1.2–8.5 × 0.7–5.2 cm; long-styled flowers with anthers included; drupes 4–5 × 5–6 mm ..... 28a. *G. obovata* var. *obovata* (Baker) Malcomber
40′. Leaves obovate or oblanceolate, 6–23.5 × 1.8–9 cm; long-styled flowers with anthers exserted; drupes 6–7 × 6–7 mm ..... 28b. *G. obovata* var. *sphaerocarpa*
39′. Bracteoles small to well developed, 1–5 mm long, with at least some > 3 mm long.
41. Pedicels 0.5–2 mm long; petioles 5–25 mm long; corolla with tube ca. 1.5 mm diam. and lobes ca. 2 mm long; 0–450 m elevation ..... 17. *G. laevis*
41′. Pedicels 2–5 mm long; petioles 3–11 mm long; corolla with tube ca. 1.2 mm diam. and lobes 3.5–4 mm long; 738–1489 m elevation ..... 33. *G. rakotovaoana*

31′. Stipules tubular.
42. Inflorescences subcapitate, spiciform, or narrowly pyramidal, without tertiary axes, with secondary axes undeveloped or developed, 2–15 mm long, and terminating in a 3- to 5-flowered cyme.
43. Inflorescences subcapitate, with axes hardly developed; stipules with 1 deep incision; corolla lobes 5 ..... 9. *G. drakeana* Aug. D.C.

43′. Inflorescences spiciform to narrowly pyramidal, with primary axis at least shortly developed; stipules without incisions or with 2 short incisions; corolla lobes 4.
44. Inflorescences pendulous on flexuous peduncles, these often produced on supra-axillary branches; stipules lobes 0.5–11 mm long . . . . . 16. *G. inflexa* Boivin ex Baill.
44′. Inflorescences erect to pendulous on straight or geniculate peduncles, these terminal on principal branches; stipule lobes 0.3–3 mm long.
45. Leaves elliptic-lanceolate, elliptic-oblong, elliptic, or obovate, most or all leaves widest at or below middle; corolla with tube 5–6 mm long, lobes 3.5–5 mm long . . . . . 7. *G. cardiocarpa* Boivin ex Baill.
45′. Leaves oblanceolate to narrowly oblanceolate, most or all leaves widest above middle; corolla with tube ca. 3.5 mm long, lobes ca. 2 mm long . . . . . 18. *G. littoralis* C. M. Taylor

42′. Inflorescences paniculiform, thyrsiform, corymbiform-rounded, or pyramidal, with secondary axes developed, 12–75 mm long, and terminating in a 5- to 7-flowered cyme and/or bearing tertiary axes.
46. Stipules with tubes 35–51 mm long, persistent, generally overlapping at consecutive nodes, with 2 interpetiolar incisions that create 2 intrapetiolar segments, the segments 15–50 mm long, acute to truncate . . . . . 26. *G. monstruosa* Malcomber
46′. Stipules with tubes 2–80 mm long, persistent or deciduous, overlapping or not at consecutive nodes, remaining entire and truncate to acute or with 1 or 2 incisions, sometimes with the 2 incisions creating 2 interpetiolar or intrapetiolar segments 10–18 mm long and acute to obtuse.
47. Leaves narrowly elliptic to oblanceolate, 29–40 × 5.3–8.4 cm; stipules with tubes 29–80 mm long; inflorescences pendulous, with peduncle 5–16 cm long; corolla with tube 18–21 mm long . . . . . 19. *G. lowryi*
47′. Leaves elliptic, narrowly elliptic, elliptic-oblong, oblanceolate, or obovate, 5.5–28 × 2–15 cm; stipules with tubes 5–25 mm long; inflorescences erect to strongly deflexed, subsessile to pedunculate with peduncle to 15 cm long; corolla with tube 2–16 mm long.
48. Corolla with tube 10–16 mm long and lobes 3.5–5.5 mm long . . . . . 2. *G. arenaria* Baker
48′. Corolla with tube 2–10 mm long and lobes 2–3 mm long.
49. Corolla tube 6–10 mm long and on at least some flowers longer than 6 mm; leaves 6–15 cm wide; calyx limb with tubular (i.e., unlobed) portion 1–2.5 mm long.
50. Calyx with tubular portion 1–1.5 mm long, truncate or lobed with lobes to 0.3 mm long; corolla tube 6.5–10 mm long; fruit 8–9 × 8–10 mm . . . . . 20. *G. macrobotrys* Baker
50′. Calyx with tubular portion 1.8–2.5 mm long, lobed with lobes 0.8–1.1 mm long; corolla tube 6–8 mm long; fruit 5–6 × 6–8 mm . . . . . 36. *G. robusta* C. M. Taylor
49′. Corolla tube 2–6 mm long; leaves 3.5–11 cm wide; calyx limb with tubular (i.e., unlobed) portion 1–3 mm long.
51. Calyx with tubular portion 1.8–3 mm long; leaves with 4 to 6 pairs of secondary veins and the tertiary venation finely reticulated and visible abaxially . . . . . 27. *G. nitida*
51′. Calyx with tubular portion 1–1.5 mm long; leaves with 5 to 9 pairs of secondary veins and the tertiary venation not visible or loosely reticulated and sparsely or only weakly visible abaxially.
52. Leaves at apex rounded to truncate, without acuminate tips or with tips 1–1.5 mm long; stipule tubes inflated; inflorescences with peduncle 2–5 cm long and branched portion 11–19 cm long . . . . . 35. *G. razakamalalana* C. M. Taylor
52′. Leaves at apex obtuse or acuminate with tips 3–10 mm long; stipule tubes loose around stem but not much inflated; inflorescences with peduncle 3–8.5 cm long and branched portion 5.5–14 cm long.
53. Corolla tubes 2–3 mm long; stipules with tubular portion 5–16 mm long . . . . 5. *G. breviflora* C. M. Taylor
53′. Corolla tubes 4–6 mm long; stipules with tubular portion 15–25 mm long . . . . . 29. *G. sclerophylla*
(Note: This species has calyptrate stipules but sometimes these can be easily confused with tubular stipules, therefore this species is keyed here under both conditions)

1. Gaertnera alata Bremek. ex Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 379, fig. 2. 2005. TYPE: Madagascar. Toamasina: Atsinanana, forêt d'Andasibe, bassin de l'Onive, Feb. 1925, *H. Perrier de la Bathie 17098* (holotype, P).

Distribution and IUCN Red List category. *Gaertnera alata* is known only from the type collection made in 1925 and two other collections made in 1999, all from the Ankilahila forest southeast of Tsinjoarivo along the border of the provinces of Toamasina and Antananarivo in central eastern Madagascar at 1400–1550 m. The type collection cannot be precisely georeferenced, but is probably in the same general vicinity as the more recent collections. Lacking any formal protection, this area of escarpment subhumid forest is subject to ongoing clearing, and therefore the species is likely to experience decline at its single known location. Thus, *G. alata* is here considered Critically Endangered (CR) due to its limited geographic range (AOO = 10 km^2) and threats to its habitat [B2ab(iii)].

See Malcomber and Taylor (2009: 600) for a species description.

2. Gaertnera arenaria Baker, J. Linn. Soc., Bot. 20: 209. 1883. *Sykesia arenaria* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. Toamasina: Atsinanana, Tranomaro near Tamatave, sands near sea, July 1862, *C. J. Meller s.n.* (holotype, K).

Distribution and IUCN Red List category. *Gaertnera arenaria* has a large geographic range (EOO = 222,903 km^2) in humid and subhumid forest from sea level to 1400 m elevation, from northern to eastern and southeastern Madagascar in the provinces of Antsiranana, Fianarantsoa, Toamasina, and Toliara. Additionally it is found in numerous protected areas (Andohahela, Lokobe, Mananara-Nord, Manongarivo, Marojejy, Masoala, Montagne d'Ambre, Nosy Mangabe, and Tsaratanana), thus *G. arenaria* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 602–603) for a species description and synonymy.

3. Gaertnera arenarioides C. M. Taylor, sp. nov. TYPE: Madagascar. Antsiranana: DIANA, Ambanja, Ambodimanga-Ramena, Antsahabe, Mandrizavona village, 13°48″S, 48°45″E, 460 m, 12 Apr. 2000, *J. Rabenantoandro, D. Ravelonarivo, F. Ratovoson & R. Razafindramanana 167* (holotype, MO-5737702!; isotypes, P n. v., TAN n. v.). Figure 1.

Haec species a *Gaertnera arenaria* Baker stipulis calyptratis unilobis atque foliorum venatione tertiaria non vel interdum manifesta, a *G. obovata* Baker alabastris acutis, foliis apice acutis vel leniter acuminatis, stipulis unilobis ad nodos summos 3 persistentibus atque domatiis ex lineis hirtellis constantibus distinguitur.

Shrubs to 5 m tall, drying brown to dark brown; branchlets 3.5–6 mm diam., flattened to subquadrangular, glabrous. Leaves opposite; blades obovate, oblanceolate, or elliptic-oblong, 12–25 × 4–7.5 cm, drying chartaceous and matte, glabrous on both surfaces, at base cuneate to obtuse or rounded, at apex acute to weakly acuminate with tips 5–10 mm; secondary veins 6 to 10 pairs, abaxially prominulous to prominent, with domatia in form of irregular patches of hirtellous pubescence along midrib and sometimes basal portions of secondary veins, with remaining venation not visible or intersecondary veins sometimes visible; petioles 7–12 mm, glabrous; stipules calyptrate, glabrous, drying papery to chartaceous and brown, generally persistent, 25–35 mm, on each side with 2 ridges or wings, these 0.2–1 mm wide and widened from top to bottom, continuing as flattened wings ca. 0.5 mm wide encircling petioles, apex with 1 well-developed incision, with 1 lobe, narrowly triangular to linear, 2.5–3 mm. Inflorescence cymose, many-flowered (50+), terminal on principal branches, erect, glabrous, sessile or pedunculate; peduncles 9–14 cm; branched portion pyramidal to narrowly pyramidal, 12–21 × 6–22 cm, branched to 3 or 4 orders, often with secondary axes very well developed; bracts narrowly triangular to lanceolate or ovate, 3–12 mm, or those subtending secondary axes sometimes foliaceous; bracteoles ovate, 1–2.5 mm. Flowers sessile, biology unknown, 5-merous; calyx cupuliform, 2.5–3 mm wide, externally and internally glabrous, tube 2–3 mm, subtruncate to denticulate or dentate, teeth 5, broadly triangular, to 0.5 mm, subequal; corolla acute in bud, at anthesis salverform, white, externally glabrous, internally densely barbate in throat and on basal portions of lobes, tube 10–12 mm, cylindrical to weakly funnelform, ca. 2 mm diam. near middle, lobes narrowly ligulate, ca. 5 mm, at apex smooth abaxially and adaxially; anthers in presumed short-styled form 3.5–4 mm, partially exserted; stigmas not seen. Drupes subglobose, ca. 8 mm diam., violet or black; pyrenes 2, hemispherical, abaxially smooth.

Habitat, distribution, and phenology. *Gaertnera arenarioides* is known from humid forests at 460–700 m in the province of Antsiranana and the region of DIANA; it has been collected in flower in April and in fruit in March.

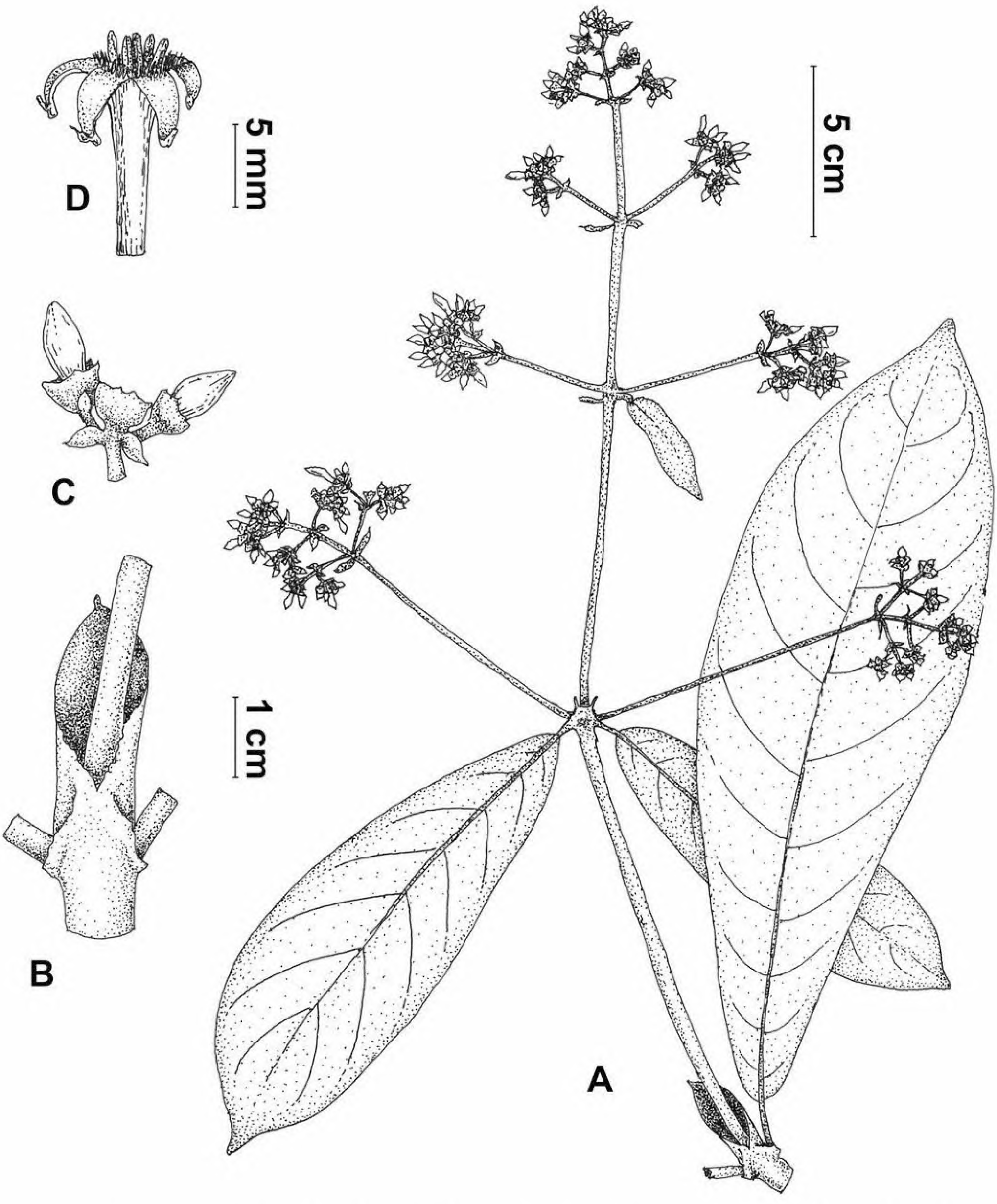


Figure 1. *Gaertnera arenarioides* C. M. Taylor. —A. Flowering branch. —B. Portion of stem, with node, stipule, and bases of two petioles. —C. Portion of inflorescence, with two flower buds and one flower from which corolla has fallen. —D. Corolla at anthesis, dissected off flower. C, D, to same 5-mm scale. Based on the type *J. Rabenantoandro et al. 167* (MO).

IUCN Red List category. *Gaertnera arenarioides* is known only from along the northern boundary of the Tsaratanana protected area, both within and outside of the protected area. The area outside of the protected area is subject to ongoing clearing and conversion for agriculture. Therefore, with a very limited geographic range (an EOO and AOO of only ca. 12 km^2), threats to its habitat outside of the protected area, and only 3 locations, *G. arenarioides* is here considered to be Endangered [EN B1ab(iii)-2ab(iii)].

Discussion. *Gaertnera arenarioides* is similar in general aspect and several features to *G. arenaria*, and has previously been confused with it; the species epithet refers to this similarity. *Gaertnera arenaria* is

found widely in Madagscar, and differs from this new species in its cylindrical tubular stipules, leaves with the tertiary venation extensively reticulated and visible, and usually longer corollas with tubes 10–16 mm (for contrasting character states of *G. arenarioides*, see its description above). This new species is also similar to *G. obovata* var. *sphaerocarpa*, which is also found widely in Madagascar and differs in its foveolate domatia, generally corymbiform inflorescences with the axes pubescent, and caducous 2-lobed stipules.

Paratypes. MADAGASCAR. **Antsiranana:** DIANA, Antsahabe, Ambanja, Réserve Nat. Intégrale de Tsaratanana, Antsahafaly River, Mandrizavona village, 13°53′S, 48°49′E, *P. Antilahimena et al. [sic, no other collectors listed] 387* (MO, P, TAN), *P. Antilahimena et al. [sic, no other collectors listed] 405* (MO, P, TAN); Antsaharatsy, *J. Rabenantoandro, D. Ravelonarivo, F. Ratovoson & P. Antilahimena 188* (K, MO, P, TAN).

4. Gaertnera bambusifolia Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 380, fig. 2. 2005. TYPE: Madagascar. Antisiranana: SAVA, Rés. Nat. Marojejy, along trail to summit of Marojejy Est, NW of Mandena, 850–1000 m, *J. S. Miller & P. P. Lowry 3978* (holotype, MO; isotypes, K, P, TAN).

Distribution and IUCN Red List category. *Gaertnera bambusifolia* is known only from two collections in northeastern Madagascar, in the province of Antsiranana and the region of DIANA at 850–1235 m. The two known mid-elevation subpopulations in subhumid forest are encompassed within the Anjanaharibe-Sud and Marojejy protected areas, respectively, and are therefore currently not subject to threat (the recent illegal exploitation of rosewood having occurred at lower elevations than this within Marojejy). Therefore, with no population decline anticipated, the species is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 604–605) for a species description.

5. Gaertnera breviflora C. M. Taylor, sp. nov. TYPE: Madagascar. Toliara: Anosy, N Ft. Dauphin (Tôlañaro), near St. Luce (Manofiafy), just behind coastal dunes, S & W of fishing village, 24°47′S, 47°10′E, 25 m, 20 Oct. 1989, *G. McPherson, N. Dumetz & R. Rabevohitra 14192* (holotype, MO-3767834!; isotypes, K. n. v., TEF n. v.). Figure 2D–F.

Haec species a *Gaertnera obovata* Baker var. *sphaerocarpa* (Baker) Malcomber stipulis tubularibis plerumque persistentibus, a *G. macrostipula* Baker calyce subtruncato denticulatove, ab ambabus corolla breviore distinguitur.

Shrubs and small trees to 10 m tall, drying brownish green or brown; branchlets 3.5–7 mm diam., quadrangular, glabrous. Leaves opposite; blades obovate, oblanceolate, elliptic, or oblong-obovate, 8–20 × 3.5–10.5 cm, drying chartaceous to subcoriaceous and matte, glabrous on both surfaces, at base obtuse to infrequently rounded or acute, at apex acute to rounded and often with acuminate tips 3–10 mm; secondary veins 5 to 7 pairs, thinly prominulous abaxially, with narrow foveolate domatia ca. 0.1–0.2 mm deeply inserted in vein axils, with intersecondary and tertiary venation not or sparsely (i.e., few veins widely scattered) visible abaxially; petioles 3–22 mm, glabrous; stipules tubular, glabrous, drying papery to chartaceous and brown, generally persistent, tube 5–16 mm, smooth, with wing flattened to rounded, 0.3–1.2 mm, encircling petioles and extending to unite with base of tube, apex truncate or with 1 or 2 incisions, with 4 narrowly triangular to linear lobes 1–5 mm, ciliolate. Inflorescences lax to somewhat congested cymose, many-flowered (50+), terminal on principal branches, erect, moderately to densely pilosulous-puberulous, pedunculate; peduncle 3–8.5 cm; branched portion pyramidal to broadly pyramidal, 5.5–10 × 5–11 cm, branched to 3 or 4 orders; bracts narrowly triangular to narrowly ligulate, 3–10 mm, or those subtending secondary axes frequently foliaceous; bracteoles ligulate to triangular or frequently 3-lobed, 1–4.5 mm. Flowers sessile or subsessile, distylous, 5-merous; calyx cupuliform, 2–2.5 mm wide, externally glabrous to puberulous at least near base, internally glabrous except with a strigillose ring near middle inside, truncate to denticulate, tube 1–1.2 mm, teeth 5, triangular, to 0.3 mm or occasionally on some flowers of an inflorescence triangular to ligulate, 0.8–1 mm (e.g., *Rabenantoandro & Morja 1594*, *Decary 10135*); corolla obtuse to rounded in bud, at anthesis salverform, white or greenish white, externally glabrous, internally barbate in upper part of tube and onto lobes, tube 2–3 mm, cylindrical to funnelform, ca. 1.2 mm diam. near middle, lobes ligulate-triangular, 2–3 mm, at apex abaxially smooth, adaxially smooth or very shortly hooked; anthers in short-styled form ca. 1.5 mm, exserted, in long-styled form 1.1–1.5 mm, partially exserted; stigmas in short-styled form ca. 1 mm, included, positioned in upper part of corolla tube, in long-styled form 0.5–1 mm, exserted. Drupes ellipsoid to obovoid and laterally sometimes somewhat flattened, 6–9 × 6–9 mm, purple-black, blue-black, or blue; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera breviflora* is known from littoral forest and low-

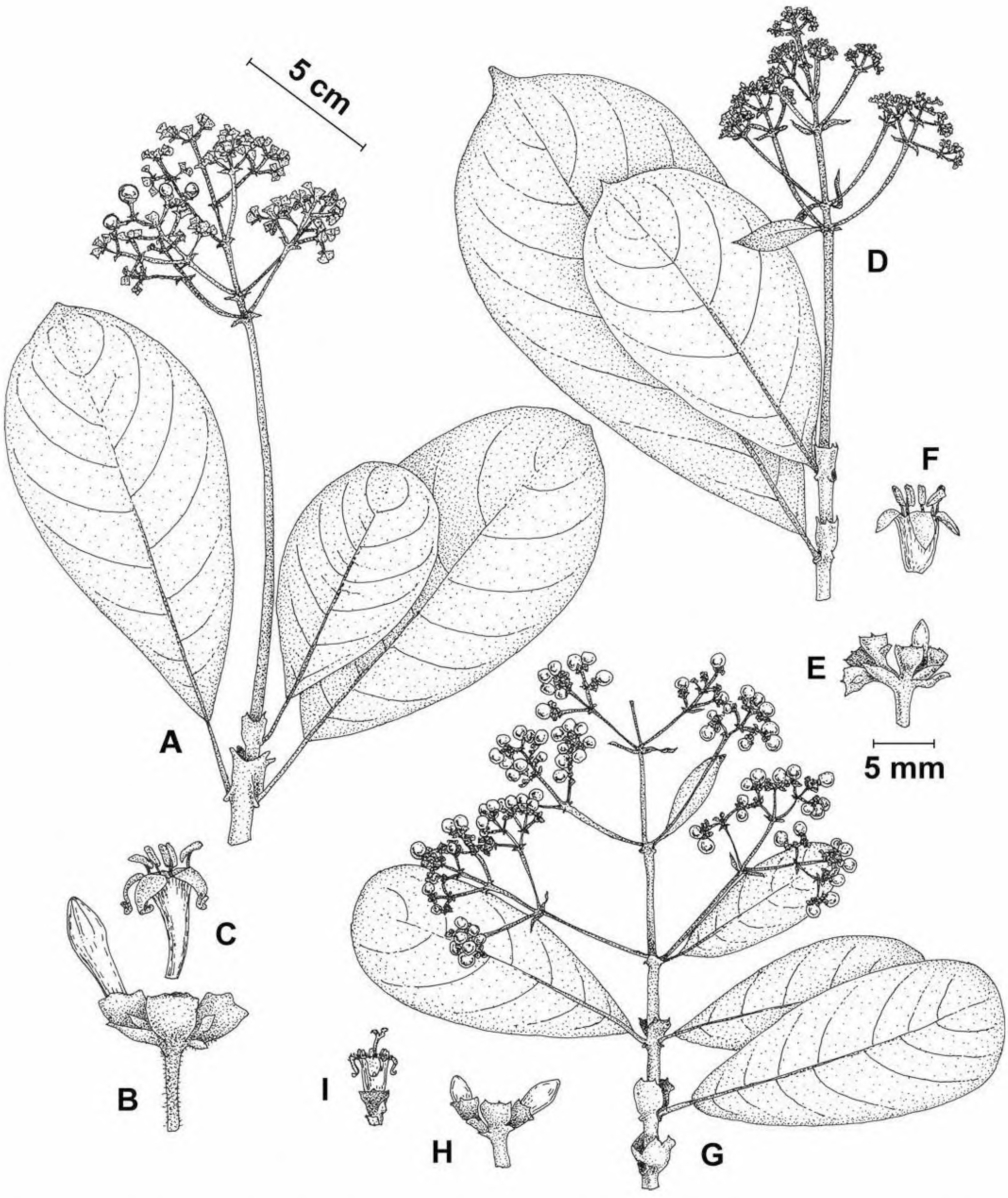


Figure 2. A–C. *Gaertnera robusta* C. M. Taylor. —A. Flowering branch, based on *M. Andrianarisata 102* (MO). —B. Portion of inflorescence, with one flower bud and two flowers from which corollas have fallen. —C. Corolla at anthesis, dissected off flower. B, C, based on the type *F. Ratovoson & F. Randiantafika 13* (MO). D–F. *Gaertnera breviflora* C. M. Taylor. —D. Flowering branch, based on *A. P. Davis et al. 1214* (MO). —E. Portion of inflorescence, with one flower bud and five flowers from which corollas have fallen. —F. Corolla at anthesis, dissected off flowers. E, F, based on the type *G. McPherson et al. 14192* (MO). G–I. *Gaertnera razakamalalana* C. M. Taylor. —G. Flowering branch, based on *Rabevohitra et al. 5011i* (MO). —H. Portion of inflorescence with two flower buds and one flower from which corolla has fallen. —I. Flower at anthesis. H–I, based on the type *G. E. Schatz et al. 3604* (MO). A, D, G, to same 5-cm scale; B, C, E, F, H, I, to same 5-mm scale.

elevation, evergreen humid forest on sand and laterite at 0–250 m in the province of Toliara and the region of Anosy and is often reported from swampy microsites. *Gaertnera breviflora* has been collected in flower in June, July, and October through December, and in fruit in January, February, October, and December.

IUCN Red List category. This species is found in the littoral forest fragments that have received

protection in conjunction with ongoing mining activities (Mandena, Petriky, Sainte Luce), but the species is nevertheless experiencing decline in other non-protected forest fragments subject to exploitation for timber and firewood. The geographic range size currently meets the threshold for Endangered (EOO = 1083 km²; AOO < 500 km²), but with seven separate locations. *Gaertnera breviflora* is here considered instead to be Vulnerable [VU, B1ab(ii,iii,iv)+2ab(ii,iii,iv)]; however, it could soon become Endangered as locations or subpopulations are lost.

Discussion. *Gaertnera breviflora* can be recognized by its well-developed, tubular, usually persistent, smooth stipules; leaves with the secondary venation generally not at all evident; thyrsiform or paniculiform inflorescences; calyx limbs that are truncate to denticulate or occasionally with one relatively larger lobe; relatively short corollas; and distribution at low elevations in southeastern Madagascar. The specific epithet refers to the relatively short corollas.

Gaertnera breviflora has been confused with *G. obovata* var. *sphaerocarpa*, which is found widely in Madagascar; however, *G. obovata* var. *sphaerocarpa* can be recognized by its spathaceous and generally caducous stipules, leaves usually with the tertiary venation visible abaxially, longer corollas with tubes 4–8 mm, and distribution generally at higher elevations, 360–1876 m (for contrasting character states of *G. breviflora*, see its description above). *Gaertnera breviflora* has also been confused with *G. arenaria*, which is found widely in Madagascar including in coastal forests; however, *G. arenaria* can be recognized by its stipules with four longitudinal ribs that extend from the base of the sheath to connect with the lobes, flowers that are mostly separated from each other on pedicels (or elongated axes) 1–5 mm long, and longer corollas with tubes 10–16 mm long. *Gaertnera breviflora* is also similar to *G. robusta* and *G. razakamalalana*; see the discussion under each of these other species for their separation from *G. breviflora*. Also similar is *G. sclerophylla*, described below and found in eastern through southeastern Madagascar, but these species differ in their stipules: tubular and truncate with the tube 5–16 mm long and four short lobes in *G. breviflora* versus calyptrate and acute with the tube 15–25 mm long and one or two lobes in *G. sclerophylla*.

Paratypes. MADAGASCAR. **Toliara:** Anosy, environs of St. Jacques, 5.4 km NNW Taolañaro, 24°59′S, 46°58′E, *A. P. Davis, J. Andrianantiana & D. Gower 1214* (K, MO); 10 km N Fort-Dauphin (Tôlañaro), forêt de Mandena, 24°57′S, 47°00–02′E, *P. De Block, F. Rakotonasolo, T. Randriamboavonjy, S. Dessein & V. Leyman 732* (BR, MO), *L. J. Dorr, L. C. Barnett, A. Rakotozafy, M. R. Cheek & N. Razafimalala 3981* (K, MO), *F. R. Fosberg 52549* (MO), *F. R. Fosberg 52553* (K, MO), *S. T. Malcomber 1175* (K, MO), *J. L. Zarucchi, E. Rakotobe, S. G. Razafimandimbison & A. Pool 7590* (K, MO); Pointe Itaperina, Dt. du Fort-Dauphin, *R. Decary 10135* (MO, P); Vinanibe, Dt. de Fort-Dauphin, *R. Decary 10745* (K, MO, P); ca. 11 km WSW Fort-Dauphin (Tôlañaro), Mananbaro, forêt de Petriky, 25°05′S, 46°52′E, *N. Dumetz, G. McPherson & R. Rabevohitra 806* (K, MO), *N. Dumetz & G. McPherson 1115* (K, MO), *R. E. Gereau, R. Rabevohitra & N. Dumetz 3367* (K, MO); above airport at Fort-Dauphin (Tôlañaro), 25°01′E, 46°57′E, *R. E. Gereau & N. Dumetz 3236* (K, MO); région de l'Anosy, Bemangidy Forest, ca. 3 km W Antsotso, along RN 12a, 65 km N Fort-Dauphin (Tôlañaro), 24°35″S, 47°13″E, *P. P. Lowry II, J. Rabenantoandro, F. Randriatafka, E. Lowry, E. Ramisy & B. Mara 6675* (MO), *P. P. Lowry II, J. Rabenantoandro, F. Randriatafka, E. Lowry, E. Ramisy & B. Mara 6742* (MO); NW of Fort-Dauphin (Tôlañaro) near rd. to Andohahela Reserve, 24°46′S, 46°53′E, *G. McPherson 14454* (MO); Fort-Dauphin (Tôlañaro), Mahatalaky, forêt de Sainte-Luce, 24°46′S, 47°10′E, *J. Rabenantoandro & A. Monja 1594* (MO); Fort-Dauphin (Tôlañaro), Ampasy, Mandena-Ambavarano, forêt d'Ambavarano, 24°56′S, 47°03″E, *R. Rajoharison & G. Tsiatrefy 23* (MO).

6. Gaertnera brevipedicellata Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 382, fig. 3. 2005. TYPE: Madagascar. Fianarantsoa: Vatovavy-Fitovinany, Ranomafana Nat. Park, Talatekely, 800–900 m, 5 Nov. 1977, *S. T. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2877* (holotype, MO; isotypes, BR, G, K, P, PRE, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera brevipedicellata* is found in southeastern Madagascar in the province of Fianarantsoa at 800–1000 m. Although it is currently known only from subhumid forest within the protected areas of Andringitra and Ranomafana, its projected occurrence within the intervening escarpment forest results in a geographic range size of EOO = ca. 2700 km² and AOO = ca. 1470 km². Because of expected decline due to habitat degradation and conversion in projected sites of occurrence outside of protected areas and only six locations known, *G. brevipedicellata* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

See Malcomber and Taylor (2009: 606–607) for a species description.

7. Gaertnera cardiocarpa Boivin ex Baill., Adansonia 12: 238. 1879. TYPE: Madagascar. Toamasina: Analanjirofo, Sainte Marie, Tanambo, Apr. 1851, *L.-H. Boivin s.n.* (holotype, P; isotypes, G, P).

Distribution and IUCN Red List category. *Gaertnera cardiocarpa* is known from northeastern Mada-

gascar in the province of Toamasina at 0–300 m. Although several subpopulations of this humid forest species are found in protected areas (Mananara-Nord, Masoala), subpopulations outside of protected areas are experiencing decline from continuing conversion of forest. With a restricted geographic range size (EOO = 1099 km²; AOO < 500 km²) and only four known locations, *G. cardiocarpa* is here considered to be Endangered [EN B1ab(ii,iii,iv)+2ab(ii,iii,iv)].

See Malcomber and Taylor (2009: 609) for a species description.

8. Gaertnera darcyana Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 384, fig. 2. 2005. TYPE: Madagascar. Toamasina: Alaotra-Mangoro, 11.9 km N of Andasibe, Mantadia Nat. Park, 930 m, 21 Nov. 1997, *S. T. Malcomber, A. Davis, D. Gower & J. Andriantiana 2921* (holotype, MO; isotypes, BR, K, P, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera darcyana* is known from north-central to south-central eastern Madagascar at 700–1400 m in the provinces of Toamasina and Fianarantsoa. It is currently known from only five collections, two of which are from protected areas (Betampona, Mantadia). This species is likely to experience decline from habitat conversion outside of protected areas, particularly at the Ambatovy nickel-mining site. Due to its restricted geographic range size (EOO = 19,150 km²; AOO = 5400 km²), *G. darcyana* is here considered to be Vulnerable [VU B1ab(iii)].

See Malcomber and Taylor (2009: 612) for a species description; the petiole length was incorrectly given there as mm, this measurement is in cm.

9. Gaertnera drakeana Aug. DC., Bull. Herb. Boissier, Sér. 2, 1: 586. 1901. TYPE: Madagascar. Toamasina: Analanjirofo, Maroa [Maroantsetra], 1897, *A. Mocquerys 273* (holotype, G).

Distribution and IUCN Red List category. *Gaertnera drakeana* is found in northeastern Madagascar in the province of Toamasina at 0–300 m. It is distributed in low-elevation humid forest from south of the Ambatovaky protected area to the Bay of Antongil and is also present in the Mananara-Nord and Masoala protected areas. With a restricted geographic range size (EOO = 4574 km²; AOO < 500 km²), expected continuing decline outside of protected areas, and only four known locations, *G. drakeana* is here considered to be Endangered [EN B1ab(ii,iii,iv)+2ab(ii,iii,iv)].

See Malcomber and Taylor (2009: 614–616) for a species description.

10. Gaertnera furcellata (Baill. ex Vatke) Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 386, fig. 2. 2005. *Psychotria furcellata* Baill. ex Vatke, Abh. Naturwiss. Vereine Bremen 9: 118. 1885. TYPE: Madagascar. s. loc., 24 Nov. 1877, *D. C. Rutenberg s.n.* (holotype, P).

Distribution and IUCN Red List category. *Gaertnera furcellata* is known from central eastern Madagascar in the former province of Toamasina at 900–1335 m. It is known only from two historical collections from the Zahamena protected area, and a recent collection from unprotected forest near Anjozorobe. With a restricted geographic range size (EOO = 727 km²; AOO < 500 km²), expected continuing decline outside of the protected area, and only two known locations, *G. furcellata* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

See Malcomber and Taylor (2009: 618–619) for a species description and synonymy.

11. Gaertnera guillotii Hochr., Annuaire Conserv. Jard. Bot. Gèneve, 11–12: 115. 1908, non *Gaertnera guillotii* (Hochr.) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2. Amsterdam 54(5): 148. 1963, hom. illeg. TYPE: Madagascar. Toamasina: Antsinanana, Vatomandry, près d'Analatsara, 3 Oct. 1903, *J. Guillot 36* (holotype, G; isotype, K).

Distribution and IUCN Red List category. *Gaertnera guillotii* is known from along generally the entire east coast of Madagascar, in the provinces of Antsiranana, Fianarantsoa, Toamasina, and Toliara at 0–920 m. This species is widely distributed and apparently common in eastern littoral and low-elevation humid forest from Fort Dauphin to Vohemar, and is present in the protected areas of Betampona, Mananara-Nord, Manombo, and Masoala. With a large geographic range size (EOO = 76,132 km²) and more than 25 locations, *G. guillotii* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 621–622) for a species description; the calyx lobe length there was incorrectly described as "2–3 mm;" this should read "0.2–0.3 mm."

12. Gaertnera hirsuta C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Analanjirofo, Maroantsetra, Anjahana, Andranofotsy, Farankaraina Forest, 15°27′S, 49°51′E, [no elevation], 20 June 2003, *P. Antilahimena 1954* (holotype, MO-6011480!; isotypes, K n. v., P n. v., TAN n. v.). Figure 3A–D.

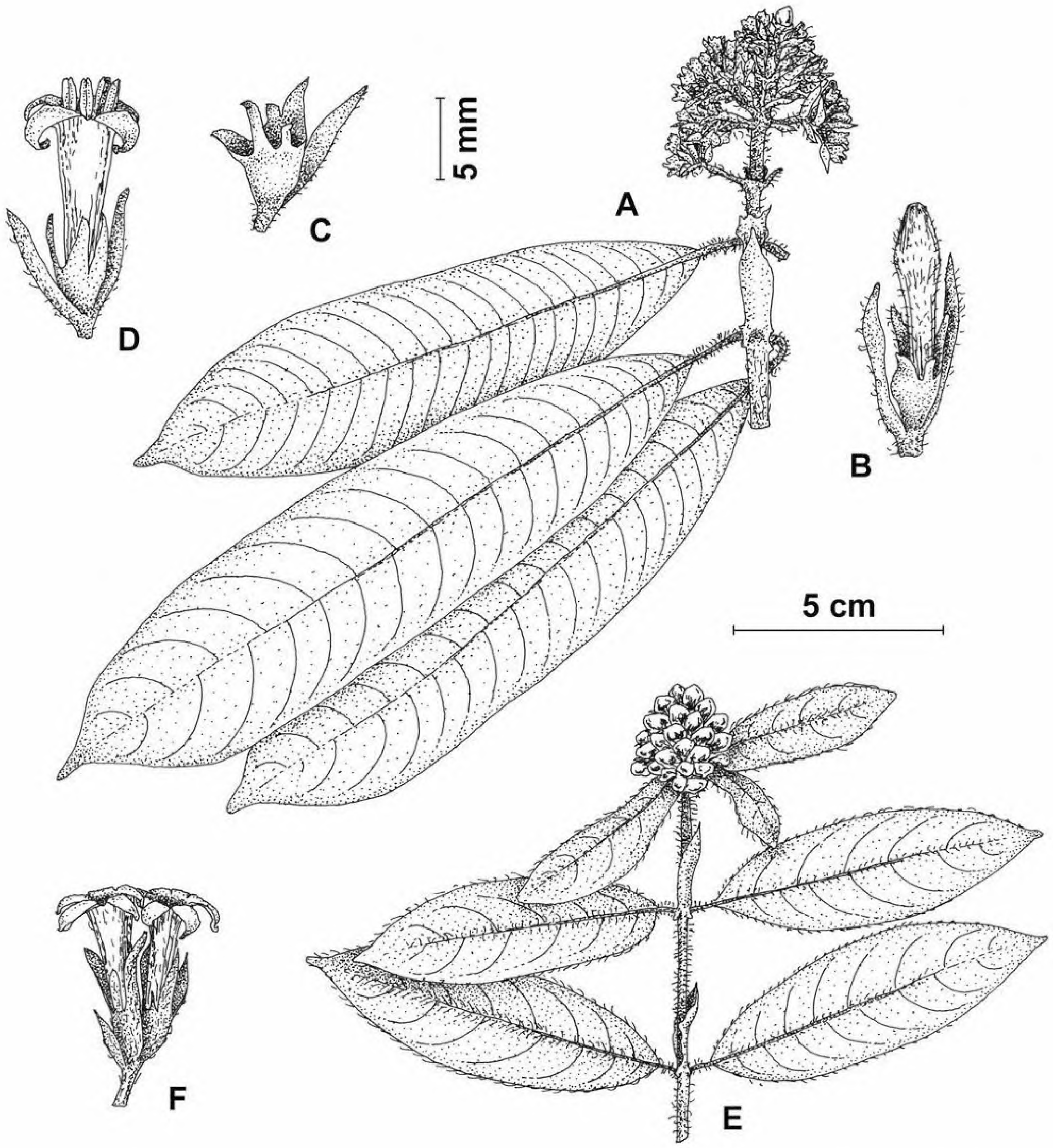


Figure 3. A–D. *Gaertnera hirsuta* C. M. Taylor. —A. Fruiting branch; based on *S. Malcomber 2833* (MO). —B. Flower bud. —C. Flower from which corolla has fallen. —D. Flower at anthesis; based on *P. Antilahimena et al. 1823* (MO). B, C, based on *D. A. Simpson 88/29* (MO). E, F. *Gaertnera phanerophlebia* Baker. —E. Fruiting branch, based on *J. Tosh 123* (MO). —F. Portion of inflorescence with two flowers at anthesis; based on *P. De Block et al. 1804* (MO). A, E, to same 5-cm scale; B–D, F, to same 5-mm scale.

Haec species a *Gaertnera ianthina* Malcomber pubescentia hirsuta, bracteolis longioribus atque calyce intus glabro lobis longioribus distinguitur.

Shrubs and small trees to 8 m tall, drying grayish green; branchlets 2.5–4 mm diam., flattened to subterete, hirsute later becoming glabrescent, the trichomes drying whitened. Leaves opposite; blades narrowly elliptic to elliptic-oblong, 11.5–22 × 2.2–6.2 cm, drying stiffly papery to chartaceous and matte, adaxially glabrous throughout or hispidulous to hispid on midrib with trichomes deciduous leaving pustulose bases, abaxially hirsute to pilose throughout or glabrous on lamina, at base cuneate to rounded, at apex abruptly narrowly acuminate with tips 5–15 mm; secondary veins 14 to 30 pairs, abaxially prominent, without domatia, with tertiary veins subparallel and prominulous abaxially; petioles 5–15 mm, hirsute to glabrescent; stipules calyptrate, hirsute to glabrescent, drying membranaceous and reddish brown, deciduous through fragmentation, 25–

60 mm, with thinly prominent ribs, with rounded wings 1.5–2.5 mm wide and developed only below petioles, apex with 1 incision, narrowly triangular, ca. 4 mm, perhaps lobed. Inflorescences subcapitate to congested cymose, many-flowered (50+), terminal on principal branches, erect, densely hirsute, subsessile to pedunculate, peduncle to 2.5 cm; branched portion broadly pyramidal to corymbiform, 4–7 × 4–8 cm, branched to 2 to 4 orders; bracts narrowly triangular to narrowly ligulate, 8–18 mm; bracteoles triangular to ligulate, 3–9 mm, often fused to base of calyx limb or inserted shortly above its base; pedicels to 2 mm. Flowers mixed sessile and pedicellate, with biology unknown, 5-merous; calyx cupuliform, 3–4 mm wide, externally hispidulous to glabrescent, internally glabrous, tube 2.5–4 mm, lobed, lobes 5, narrowly triangular, 1.5–6 mm, unequal with variously 1 to 3 lobes more than twice as long as shortest lobe; corolla in bud obtuse, at anthesis funnelform, white, externally hirsute at least in upper 1/2–2/3, internally not seen, tube ca. 11 mm, funnelform, ca. 2.5 mm diam. near middle, lobes triangular, ca. 5.5 mm, at apex a little thickened abaxially, smooth adaxially; anthers in presumed short-styled form ca. 3 mm, exserted; stigmas not seen. Drupes subglobose to subglobose-ovoid, 6–8 mm diam., becoming white then blue-black; pyrenes 2, hemispherical, abaxially smooth to angled or with 3 or 4 longitudinal sulci.

Habitat, distribution, and phenology. *Gaertnera hirsuta* is known from humid forests at 0–600 m in the Masaola Peninsula region of province of Toamasina and the region of Analanjirofo, often near streams and rivers. *Gaertnera hirsuta* has been collected in flower in January, February, and August and in fruit in July, August, and October, often concurrently with the flowers.

IUCN Red List category. *Gaertnera hirsuta* is known from the Bay of Antongil region including the Masoala protected area. With expected continuing decline outside of the protected area due to habitat conversion, a restricted geographic range size (EOO = 563 km²; AOO < 500 km²), and only four known locations, *G. hisuta* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

Discussion. This new species is characterized by its distinctive hirsute pubescence, and the species epithet refers to this. *Gaertnera hirsuta* is very similar in aspect and drying color to *G. ianthina* Malcomber, which is found widely in Madagascar; *G. ianthina* differs in its appressed strigose pubescence; generally shorter petioles, 4–9 mm; leaves often with fewer secondary veins, in 14 to 20 pairs; shorter bracteoles, 0.1–2 mm; calyx with a ring of trichomes in the interior and shorter lobes, 0.5–2.5 mm; and pink to purple shorter corollas, with the tube 7–9 mm long (for contrasting character states of *G. hirsuta*, see its description above). However, *G. hirsuta* has been primarily confused with *G. phanerophlebia* Baker, and the illustration of *G. phanerophlebia* presented by Malcomber and Taylor (2009: 623, fig. 11G–M) actually represents *G. hirsuta*. Accordingly a revised description and an illustration (Fig. 3E, F) of *G. phanerophlebia* are presented in this article. *Gaertnera phanerophlebia* is found in northern to east-central Madagascar and can be separated from this new species by its smaller leaves, 3–14.5 × 1.4–4.5 cm, with fewer secondary veins, in 6 to 15 pairs, and the tertiary venation not visible; capitate to only shortly cymose inflorescences; reddish brown drying color; and shorter corolla lobes, ca. 3 mm.

Paratypes. MADAGASCAR. **Toamasina:** Analanjirofo, Maroantsetra, Ambinanitelo, Soanafindra, Anjanaharibe forest, 15°11′S, 49°37′E, *P. Antilahimena, Pascal & Ramaroson 1823* (MO, P, TAN); Maroantsetra, Andranofotsy river, E of village of Sahavary, *D. A. Simpson 88/29* (K, MO); Andronobe, Masoala Peninsula, Masaola Nat. Park, W coast, Andranobe, *Möise & Solo 10* (MO, P, TAN), *Möise & Solo 10A* (MO, P, TAN), beside Andranobe River, *S. T. Malcomber 2830* (K, MO, P, TAN), 3.8 km E of Andranobe, Be Dinta Camp, 15°40′S, 49°58–59′E, *S. T. Malcomber 2833* (K, MO, P, TAN), *M. L. Zjhra & J. Hutcheon 445* (K, MO, P, TAN); Masaola Peninsula, S of village of Ambanizana in Andranobe River watershed, 15°40′S, 49°58′E, *N. Vasey & N. Velo 32* (K, MO, P, TAN).

13. Gaertnera hispida Aug. DC., Bull. Herb. Boissier, Sér. 2, 1: 585. 1901. TYPE: Madagascar. Toamasina: Analanjirofo, Maroa [Maroantsetra], *A. Mocquerys 155* (lectotype, designated by Malcomber & Taylor [2009: 623], G-DC).

Distribution and IUCN Red List category. *Gaertnera hispida* is found in northeastern Madagascar in the provinces of Antsiranana and Toamasina at 0–300 m. It occurs in lowland humid forest from the Mananara-Nord protected area to the Bay of Antongil, including in the Masoala protected area. With expected continuing decline outside of the protected areas due to habitat degradation and conversion, a restricted geographic range size (EOO = 2822 km²; AOO ca. 1000 km²), and only eight locations, *G. hispida* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

See Malcomber and Taylor (2009: 622–624) for a species description.

14. Gaertnera humblotii Drake, Bull. Soc. Bot. France 45: 352. 1899, as "Humbloti." TYPE:

Madagascar. "N. E. Madagascar," *L. Humblot 655* (holotype, P; isotypes, MO, P, WU).

Distribution and IUCN Red List category. *Gaertnera humblotii* is found in east-central to northeastern Madagascar at 0–600 m in the provinces of Antsiranana and Toamasina. It is known from humid lowland forests from west of Brickaville to Marojejy. Although it is present in the protected areas of Marojejy, Masoala, and Zahamena, the subpopulations outside of protected areas are expected to experience continuing decline due to forest degradation and clearing. Therefore, with a restricted geographic range size (EOO = 18,021 km^2), and only 10 locations, *G. humblotii* is here considered to Vulnerable [VU B1ab(iii)].

Discussion. See Malcomber and Taylor (2009: 624) for a species description. This species was characterized there by its calyx with well-developed, unequal, generally spathulate lobes 5–7 mm long. However, some recent collections (e.g., *Andrianarisata et al. 158*, MO) have some calyx lobes that are shorter than this, to as short as 3.5 mm; these updated measurements are used in the Key to Species here.

15. Gaertnera ianthina Malcomber, Ann. Missouri Bot. Gard. 96(4): 624, fig. 5G, H. 2009. TYPE: Madagascar. Antsiranana: SAVA, Marojejy Nat. Reserve, near camp 2 on summit trail, 800–1000 m, 17 Sep. 1997, *S. T. Malcomber 2773* (holotype, MO; isotypes, A, BR, G, K, P, PRE, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera ianthina* is found in northern and northeastern Madagascar, in the provinces of Mahajanga, Antsiranana, and Toamasina at 0–1700 m. It is widely distributed in humid to subhumid forest from Mananara-Nord and the Bay of Antongil across the northern mountains to the Sambirano region and is present in the protected areas of Anjanaharibe-Sud, Mananara-Nord, Manongarivo, Marojejy, Masoala, and Tsaratanana. With a large geographic range size (EOO = 25,116 km^2) and more than 25 locations, *G. ianthina* is here considered to be of Least Concern (LC).

Discussion. See Malcomber and Taylor (2009: 624–625) for a species description. This species is similar in general aspect and many details to *Gaertnera hirsuta*; see the discussion of that species for their distinction, above.

16. Gaertnera inflexa Boivin ex Baill., Adansonia 12: 237–238. 1879. TYPE: Madagascar. Toamasina: Analanjirofo, ad S.-Mariam, Tafondrou, Jan. 1848, *L.-H. Boivin 1778* (lectotype, designated in Malcomber & Taylor [2009: 625], P; isolectotype, G).

Distribution and IUCN Red List category. *Gaertnera inflexa* is known from northeastern to east-central Madagascar, in the provinces of Antsiranana and Toamasina at 0–520 m. It is widely distributed in humid forest from Mahanoro to the Masoala peninsula and is present in the protected areas of Ambatovaky, Mananara-Nord, Masoala, and Nosy Mangabe as well as the conservation site of Analalava. With a large geographic range size (EOO = 25,757 km^2) and 13 locations, *G. inflexa* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 625–626) for a species description and synonymy.

17. Gaertnera laevis C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Analanjirofo, 3–4 km W of Maroantsetra along Rte. Nationale 4, 15°28′S, 49°42′E, 10 m, 1 Dec. 1987, *G. E. Schatz & J. F. Villiers 1811* (holotype, MO-3637804!; isotypes, K n. v., P n. v., TAN n. v.). Figure 4A–C.

Haec species a *Gaertnera obovata* var. *sphaerocarpa* (Baker) Malcomber foliis elliptico-oblongis ad elliptico-oblanceolatis basi obtusis usque rotundatis, alis petiolos circumcinctis reductis atque bracteis bene evolutis distinguitur.

Small trees to 12 m tall, drying brown; branchlets 3–4 mm diam., quadrangular, glabrous. Leaves opposite; blades elliptic-oblong to elliptic-oblanceolate, 10.5–20 × 3.5–6.5 cm, drying papery to chartaceous and matte, glabrous on both surfaces, at base obtuse to rounded, at apex rounded to obtuse then abruptly acuminate with tips 5–10 mm; secondary veins 5 to 10 pairs, thinly prominulous abaxially, usually with foveolate domatia 0.2–0.5 diam., with intersecondary and tertiary venation at least weakly visible abaxially; petioles 5–25 mm, glabrous; stipules calyptrate, glabrous, drying membranceous and reddish brown, caducous and sometimes fragmenting, 30–60 mm, apparently smooth, with wings absent or encircling only lower part of petiole, rounded, up to 0.5 mm wide, apex with 1 incision, with 2 linear lobes ca. 2 mm. Inflorescences laxly cymose, many-flowered (50+), terminal on principal branches, erect, sparsely to densely puberulous-hirtellous to pilosulous with pubescence often in patches or lines, pedunculate; peduncle 3–6 cm; branched portion pyramidal, 8–18 × 10–18 cm, branched to 3 to 5 orders; bracts narrowly lanceolate, narrowly ligulate, or narrowly elliptic, 4–50 mm, or

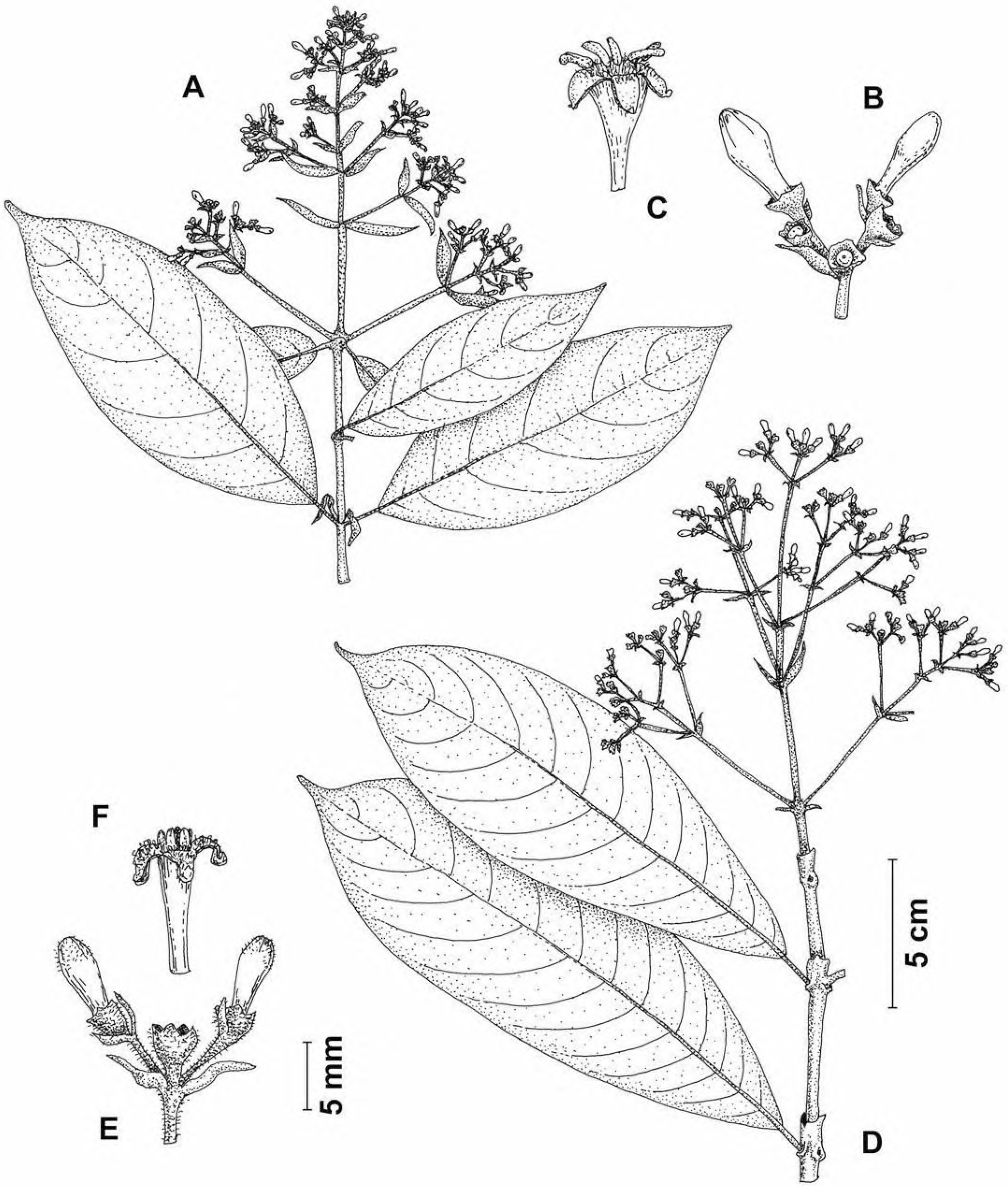


Figure 4. A–C. *Gaertnera laevis* C. M. Taylor. —A. Flowering branch; based on *G. E. Schatz & E. Carlson 2842* (MO). —B. Portion of inflorescence, with two flower buds and three flowers from which corollas have fallen. —C. Corolla at anthesis, dissected off flower. B, C, based on the type *G. E. Schatz & J. F. Villiers 1811* (MO). D–F. *Gaertnera rakotovaoana* C. M. Taylor; based on the type *C. Rakotovao et al. 2707* (MO). —D. Flowering branch. —E. Portion of inflorescence with two flower buds and one flower from which corolla has fallen. —F. Corolla at anthesis, dissected off flower. A, D, to same 5-cm scale; B, C, E, F, to same 5-mm scale.

those subtending basalmost secondary axes sometimes foliaceous and stipitate; bracteoles triangular to ovate or 3-lobed, 1–5 mm, often fused to base or lower part of calyx tube; pedicels to 2 mm. Flowers sessile to subsessile and sometimes also pedicellate, distylous, 5-merous; calyx cupuliform, 1.5–2.5 mm wide, glabrous externally and internally, tube 1–1.8 mm, often with upper portion markedly paler and thinner in texture, truncate to denticulate, teeth 4 or 5, triangular, 0.2–0.5 mm and subequal or sometimes on some flowers, 1 tooth 0.8–1.5 mm; corolla in bud obtuse, at anthesis salverform, white flushed with

lavender, externally glabrous, internally densely pilosulous on upper part of tube and onto lobes, tube 7.5–8 mm, cylindrical to funnelform, ca. 1.5 mm diam. near middle, lobes triangular to ligulate, ca. 2 mm, at apex abaxially a little thickened, adaxially with thickened hook; anthers in short-styled form ca. 2 mm, exserted, in long-styled form not seen; stigmas in short-styled form 1–1.2 mm, positioned in or just below corolla throat, in long-styled form ca. 0.4 mm, well exserted. Drupes ovoid to ellipsoid, 8–10 × 5–8 mm, mature color not noted or possibly green; pyrenes 2, hemispherical, smooth abaxially.

Distribution, habitat, and phenology. *Gaertnera laevis* is known from humid forests at 0–450 m in the provinces of Antisiranana (SAVA) and Toamasina (Analanjirofo). *Gaertnera laevis* has been collected in flower in November and December and in fruit in February, March, September, and November.

IUCN Red List category. *Gaertnera laevis* is known from the Bay of Antongil region including the Masoala and Nosy Mangabe protected areas. With expected continuing decline outside of the protected areas due to habitat degradation and conversion, a restricted geographic range size (EOO = 1415 km^2; AOO ca. 900 km^2), and only nine known locations, *G. laevis* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera laevis* can be recognized by the combination of its thin-textured calyptrate stipules without wings or with the wings reduced and only encircling the lower part of the petioles; relatively large, petiolate, elliptic-oblong to elliptic-oblanceolate leaves that are obtuse to rounded at the base; paniculiform, usually lax, rather large inflorescences; and slender, white to pale lavender corollas with rather well-developed tubes. The species epithet refers to the smooth attachment of the petioles with the stem, generally without developed wings or stipular ridges. *Gaertnera laevis* also has well-developed bracts, in particular those subtending the basalmost node or several basalmost nodes of the inflorescence. These are often foliaceous and narrowed to a stipitate (or petiolate) base. One specimen, *McPherson & Rabenantoandro 18383*, has an inflorescence with numerous foliaceous bracts at nodes without flowers, or depending on morphological interpretation, alternatively in having the stems branched to several orders with each of these branches bearing reduced leaves at three to five nodes and terminating in a small inflorescence, 2–3 × 2–3 cm and branched to only two orders.

The plants included here in *Gaertnera laevis* were previously included by Malcomber and Taylor (2009) within the circumscription of *G. obovata* var. *sphaerocephala*, based on their well-developed calyptrate stipules and generally similar flowers. However, *G. obovata* var. *sphaerocephala* is circumscribed more narrowly here. This variety is found widely in Madagascar and can be separated from *G. laevis* by its oblanceolate to obovate leaves that are cuneate to acute at the base, stipules with developed basal ridges that extend into wings and at least partially encircle the petioles, usually smaller inflorescences with the branched portion 2–13 × 4–18 cm, and generally smaller bracts, 1.5–8 mm, and bracteoles, 1–2 mm (for contrasting characters of *G. laevis*, see its description above). Additionally *G. obovata* var. *sphaerocephala* usually has corollas with the tube 2–2.5 times as long as the lobes versus the corolla tube ca. 4 times as long as the lobes in *G. laevis*.

Paratypes. MADAGASCAR. **Antsiranana:** SAVA, Parc National de Masoala, 22 km de la ville d'Ampanavoana, sur la route d'Ifasina, 15°41′S, 50°15′E, *J. Aridy & G. Rahajasoa 103* (MO); Ambodilaitra, Vinanivao, Antalaha, presqu'île de Masoala, 15°59′S, 50°11′E, *J. Rabe, G. M. Rahajasoa & Roger 183* (MO). **Toamasina:** Analanjirofo, Parc Nat. Masoala, Maroantsetra, Ambanizana, 15°43′S, 49°58′E, *J. Aridy & J. Toly 283* (K, MO); SE of village of Ambanizana, along ridge SE of Androka River, SE of Maroantsetra, NW coast Masoala Peninsula, *P. P. Lowry II, A. Rakotozafy & M. F. Nicoll 4132* (K, MO); Masoala Peninsula, S of Ambizana, Andronabe permanent plot, 15°31′S, 59°58′E, *S. T. Malcomber, F. Andriatsifera, J. Gerard & Moise 2735A* (MO); Masoala Nat. Park, W coast, near Andranobe, trail S Androka River, 15°38′S, 49°58′E, *S. T. Malcomber 2819* (MO); Masoala Peninsula, Andranobe, S of Ambanizana, 15°41′S, 49°58′E, *G. McPherson, P. Harimalala, P. Hoffmann & T. Robinson 17569* (MO); Ambanizana, 15°38′S, 49°58′E, *Möise 7* (MO); Morantsetra, Tampolo, Péninsule Masoala, entre Ambodiforaha & Laotrozo, 15°42′S, 49°59′E, *P. Poncy, S. Rapanarivo, F. Mathias & J. Y. Serein 1563* (K, MO, P); Masoala Peninsula, S of village of Ambanizana in Andranobe River watershed, 15°40′S, 49°58′E, *J. Rabe, N. Vasey, F. Andrianatsiferana & N. Veb 34* (MO); Parc Nat. Masoala, Antalavia, 15°47′S, 50°02′E, *G. Rahajasoa, R. Bernard & J. Rabe 988* (MO); massif of Ankirindo, ca. 25 air-km NW Maroantsetra via Antainambalana then Vohimaro rivers, 15°18′S, 49°33′E, *G. E. Schatz, P. P. Lowry II, J. Rabenantoandro, R. Bernard & G. Modeste 3888* (MO); Nosy Mangabe island in Bay of Antongil, 5 km S Maroantsetra, 15°30′S, 49°46′E, *G. E. Schatz & J. F. Villiers 1824* (K, MO), *G. E. Schatz & E. Carlson 2842* (K, MO).

18. Gaertnera littoralis C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Analanjirofo, Soanierana-Ivongo, comune rural Manopana, 16°46′S, 49°43′E, 2 Feb. 2003, *R. Rabevohitra, J. Rabenantoandro & R. Razakamalala 4350*

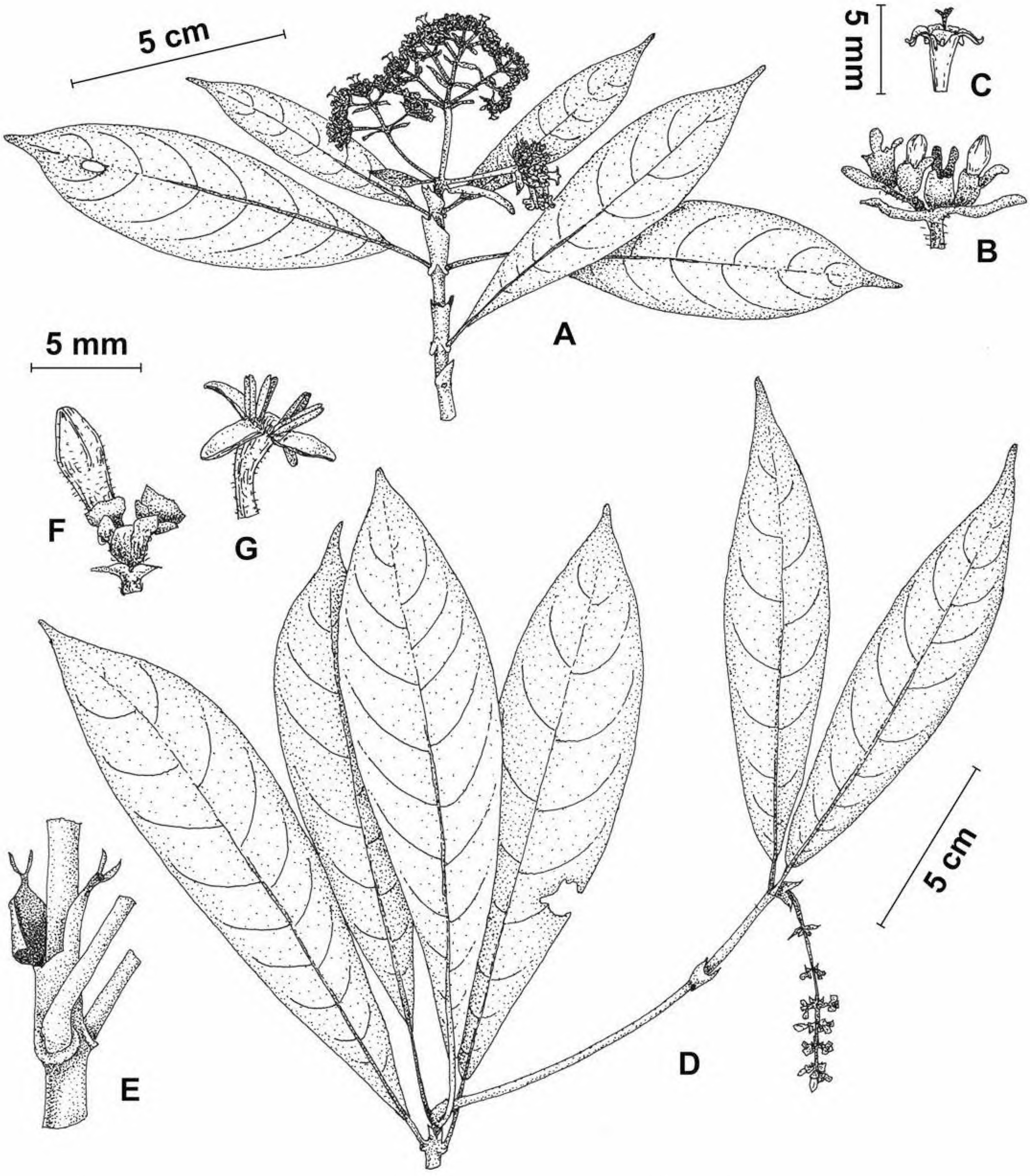


Figure 5. A–C. *Gaertnera masoalana* C. M. Taylor; based on *Moïse 4* (MO). —A. Flowering branch. —B. Portion of inflorescence with two flower buds and two flowers from which corollas have fallen. —C. Corolla at anthesis, dissected off flower together with style. D–G. *Gaertnera littoralis* C. M. Taylor. —D. Flowering branch, based on *G. E. Schatz et al. 3669* (MO). —E. Portion of stem with node, basal parts of two petioles, and stipule, based on *R. Razakamalala et al. 755* (MO). —F. Portion of inflorescence with one flower bud and one flower from which corolla has fallen. —G. Corolla at anthesis, dissected off flower. F, G, based on the type *R. Rabevohitra et al. 4350* (MO). B, C, E to same 5-mm scale; F, G to same 5-mm scale.

(holotype, MO-04845541!; isotypes, P n. v., TAN n. v.). Figure 5D–G.

Haec species a *Gaertnera cardiocarpa* Boivin ex Baill. foliis oblanceolatis ad angustioribus oblanceolatis venatione tertiaria non manifesta atque corolla breviore distinguitur; etiam sylvas littorales ad substrata arenosa plerumque habitat.

Shrubs and small trees to 4 m tall, drying brown; branchlets 2–3 mm diam., weakly quadrate to terete, glabrous. Leaves opposite; blades oblanceolate to narrowly oblanceolate, 5–17 × 1–4 cm, drying chartaceous and matte, glabrous on both surfaces, at base acute, at apex acuminate with tips 8–15 mm; secondary veins 6 to 11 pairs, plane or thinly prominulous abaxially, without domatia, with remain-

ing venation not visible abaxially; petioles 3–15 mm, glabrous; stipules tubular, glabrous, drying membranaceous to papery and brown, glabrous, persistent or deciduous via fragmentation, tube 7–11 mm, with thin ridges extending from lobes to petioles, with flat to rounded ridges 0.3–0.5 mm wide encircling petioles, at apex with 1 incision, with lobes 4, linear, 1.5–3 mm, strigillose to glabrous. Inflorescences cymose, several- to many-flowered (15 to 40), terminal on principal branches, deflexed to pendulous, glabrous, subsessile to pedunculate, peduncles to 2.5 cm; branched portion narrowly pyramidal, 1–4 × 1–2 cm, branched to 1 or 2 orders; bracts ovate or 3-lobed, 1–2 mm, often membranaceous, or those subtending basalmost secondary axes sometimes stipuliform; bracteoles ovate to deltate, 1–1.5 mm. Flowers sessile or subsessile, biology unknown, 4-merous; calyx cupuliform, 1–2 mm wide, externally glabrous, internally with a sparsely to densely pubescent ring or ridge near middle, tube 1–1.2 mm, truncate to denticulate, teeth 4, minute; corolla in bud obtuse to acute, at anthesis salverform, white, glabrous to puberulous or sparsely hirtellous externally, internally barbate in throat, tube ca. 3.5 mm, cylindrical to narrowly funnelform, ca. 0.8 mm diam. near middle, lobes narrowly ligulate, ca. 2.2 mm, at apex abaxially a little thickened, abaxially generally smooth; anthers in presumed short-styled form ca. 2 mm, shortly exserted; stigmas in presumed short-styled form ca. 0.8 mm, included, positioned just above base of corolla tube. Drupes subglobose, ca. 8 × 8 mm, black; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera littoralis* is known from littoral and humid lowland forest on sand substrates at 8–50 m in the provinces of Antsiranana (SAVA) and Toamasina (Analjarifo and Atsinanana). *Gaertnera littoralis* has been collected in flower in February, October, and November and in fruit in May.

IUCN Red List category. *Gaertnera littoralis* is known from only five collections from Mangalimaso, west of Foulepointe, to the Masoala Peninsula. With a very restricted geographic range size (EOO = 3965 km²; AOO ca. 200 km²), expected continuing decline outside of the Masoala protected area because of habitat degradation and conversion, and only three locations, *G. littoralis* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera littoralis* is known from several habitats including littoral forests, and the species epithet refers to this particular habitat. It is similar in general aspect to *G. drakeana*, which is found from northeastern Madagascar to the Bay of Antongil region; *G. drakeana* differs in its subcapitate to only very shortly branched inflorescences, generally larger calyx 2–3.5 mm wide, 5-merous flowers, larger corollas with tubes 5–6 mm and lobes 4–7 mm, and habitat in humid forest on nonsand substrates (for contrasting characters of *G. littoralis*, see its description above). *Gaertnera littoralis* is also similar to *G. cardiocarpa*, which is also found from northeastern Madagascar to the Bay of Antongil region; *G. cardiocarpa* differs in its leaves that are generally widest at the middle and have the secondary and tertiary venation well developed and visible, inflorescences with regularly developed tertiary axes, larger corollas with tubes 5–6 mm and lobes 3.5–5 mm long, and habitat in humid forest on nonsand substrates.

Paratypes. MADAGASCAR. **Antsiranana:** SAVA, Masoala Peninsula, 3 km SW of "Tamany Fred," watershed of the Anaovandrano River, 15°46′S, 50°12′E, *G. E. Schatz, J. Dransfield, S. Dransfield & R. Bernard 3669* (MO, P, TAN). **Toamasina:** Analanjirofo, N of Soanierana-Ivongo, Mamambao, near village of Antanambao-Ambodimanga, 16°45–46′S, 49°43′E, *G. McPherson, J. Rabenantoandro & R. Razakamalala 18952* (MO, P, TAN), *R. Razakamalala, D. Rabehevitra, S. N. Andrianarivelo & M. Fotsy 755* (MO, P, TAN). Atsinanana: Mangalimaso, a l'O de Foulpointe, *Capuron in Service Forestier 22095* (MO, P).

19. Gaertnera lowryi Malcomber, Ann. Missouri Bot. Gard. 96(4): 632–633, fig. 7C–H. 2009. TYPE: Madagascar. Toamasina: Analanjirofo, Masaola Nat. Park, West Coast, near Antalavia, 0.8 km NE of village, lowland forest beside Antalavia River, 50–150 m, 12 Oct. 1997, *S. T. Malcomber 2827* (holotype, MO; isotypes, BR, G, K, P, PRE, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera lowryi* is known from northeastern Madagascar, in the province of Toamasina at 0–490 m. It is known from lowland humid forest from Mananara-Nord to the Bay of Antongil region and is present in the protected areas of Makira, Mananara-Nord, and Masoala. With a restricted georaphic range size (EOO = 3514 km²; AOO ca. 300 km²), expected continuing decline outside of the protected areas because of habitat degradation and conversion, and only seven known locations, *G. lowryi* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

See Malcomber and Taylor (2009: 632–633) for a species description.

20. Gaertnera macrobotrys Baker, J. Linn. Soc., Bot. 20: 208. 1883. TYPE: Madagascar. "Cen-

tral Madagascar," *R. Baron 1945* (holotype, K; isotype, P).

Distribution and IUCN Red List category. *Gaertnera macrobotrys* is known from northeastern to southeastern Madagascar, in the provinces of Antsiranana, Toamasina, and Fianarantsoa at 50–1100 m. It is widely distributed in humid to subhumid forest up to 1000 m elevation from Vohipeno to Marojejy, and is present in the protected areas of Analamazaotra-Périnet, Marojejy, Masoala, and Ranomafana. With a large geographic range size (EOO = 47,946 km^2; AOO ca. 18,000 km^2), in spite of only nine known locations, *G. macrobotrys* is here considered to be of Least Concern [LC].

See Malcomber and Taylor (2009: 633–634) for a species description and synonymy.

21. Gaertnera macrostipula Baker, J. Linn. Soc., Bot. 20: 207. 1883. Madagascar. "Central Madagascar," *R. Baron 1922* (lectotype, designated by Malcomber & Taylor [2009: 634], K; isolectotypes, K, P).

Distribution and IUCN Red List category. *Gaertnera macrostipula* is found from northern to southeasten Madagascar in the provinces of Antsiranana, Toamasina, and Fianarantsoa at 0–2000 m. It is widely distributed in humid to subhumid to montane forests. With a large geographic range size (EOO = 183,361 km^2) and its presence in numerous protected areas (Analamazaotra-Périnet, Anjanaharibe-Sud, Betampona, Manombo, Manongarivo, Mantadia, Marojejy, Masoala, Ranomafana, and Zahamena), *G. macrostipula* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 634–635) for a species description and synonymy. The description there corresponds to the circumscription of the species here, but some specimens that were previously included in *Gaertnera macrostipula* are here excluded and classified instead in the newly described species *G. sclerophylla*, *G. velutina*, and *G. robusta*. The distinctions among these are discussed under each of these newly described spcies. *Gaertnera macrostipula* as circumscribed here is found in a variety of habitats, and can be recognized by its well-developed persistent stipules with the tube often inflated, generally covering most or all of the internode above it and becoming marcescent along the margins; calyx with well-developed lobes 1–3.5 mm; and usually larger flowers with corolla tubes 6.5–9 mm. Malcomber and Taylor (2009) described the calyces of *G. macrostipula* as variously lobed or truncate, but as circumscribed here *G. macrostipula* has lobed calyces, and the plants with truncate or subtruncate calyces are here included in *G. sclerophylla* and *G. nitida*.

22. Gaertnera madagascariensis (Hook. f.) Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 388, figs. 4, 5. 2005. *Hymenocnemis madagascariensis* Hook. f., Gen. Pl. 2: 133. 1873. TYPE: Madagascar. s. loc., *W. Bojer s.n.* (holotype, K).

Distribution and IUCN Red List category. *Gaertnera madagascariensis* is known from northeastern to southeastern Madagascar in the provinces of Antsiranana, Toamasina, Antananarivo, and Fianarantsoa at 850–1600 m. It is widely distributed in subhumid forest around the eastern escarpment. With a large geographic range size (EOO = 40,923 km^2) and its presence in the protected areas of Analamazaotra-Périnet, Andringitra, Anjanaharibe-Sud, and Ranomafana, *G. madagascariensis* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 635) for a species description and synonymy.

23. Gaertnera malcomberiana C. M. Taylor, sp. nov. TYPE: Madagascar. Antsiranana: SAVA, Anjanaharibe-Sud, Takhtajania trail, 14°45′S, 49°29′E, 1006 m, 14 Feb. 2006, *J. Tosh, P. De Block, F. Rakotonasolo & Ravenlonarivo 383* (holotype, MO-04812789!; isotypes, BR n. v., K n. v., P n. v., TAN n. v., UPS n. v.). Figure 6A, B.

Haec species a *Gaertnera ianthina* Malcomber foliis obovatis oblanceolatisve pubescentia adpressa aparenter arachnoidea sericea indutis distinguitur.

Shrubs to 6 m tall, drying grayish brown; branchlets 4–5 mm diam., flattened, strigillose with trichomes drying white to glabrous, with epidermis quickly becoming corky and thickened. Leaves opposite or ternate; blades obovate to oblanceolate, 14–21 × 4–8.8 cm, drying stiffly papery to chartaceous and matte, adaxially glabrous, abaxially glabrous on lamina and densely tangled-sericeous or lanose on midrib, secondary veins, and sometimes tertiary veins with trichomes often drying whitened and sometimes tardily deciduous, at base acute then sometimes shortly abruptly rounded, at apex obtuse to rounded then abruptly acuminate with tips 3–6 mm; secondary veins in 12 to 17 pairs, abaxially prominent, without domatia, with tertiary veins subparallel and prominulous abaxially; petioles 3–12 mm, glabrous; stipules calyptrate, glabrous, drying membranaceous and reddish brown, deciduous via fragmentation, 18–20 mm, perhaps smooth, with wings 1–2 mm wide encircling petioles and quickly becoming corky and thickened, at apex with 1

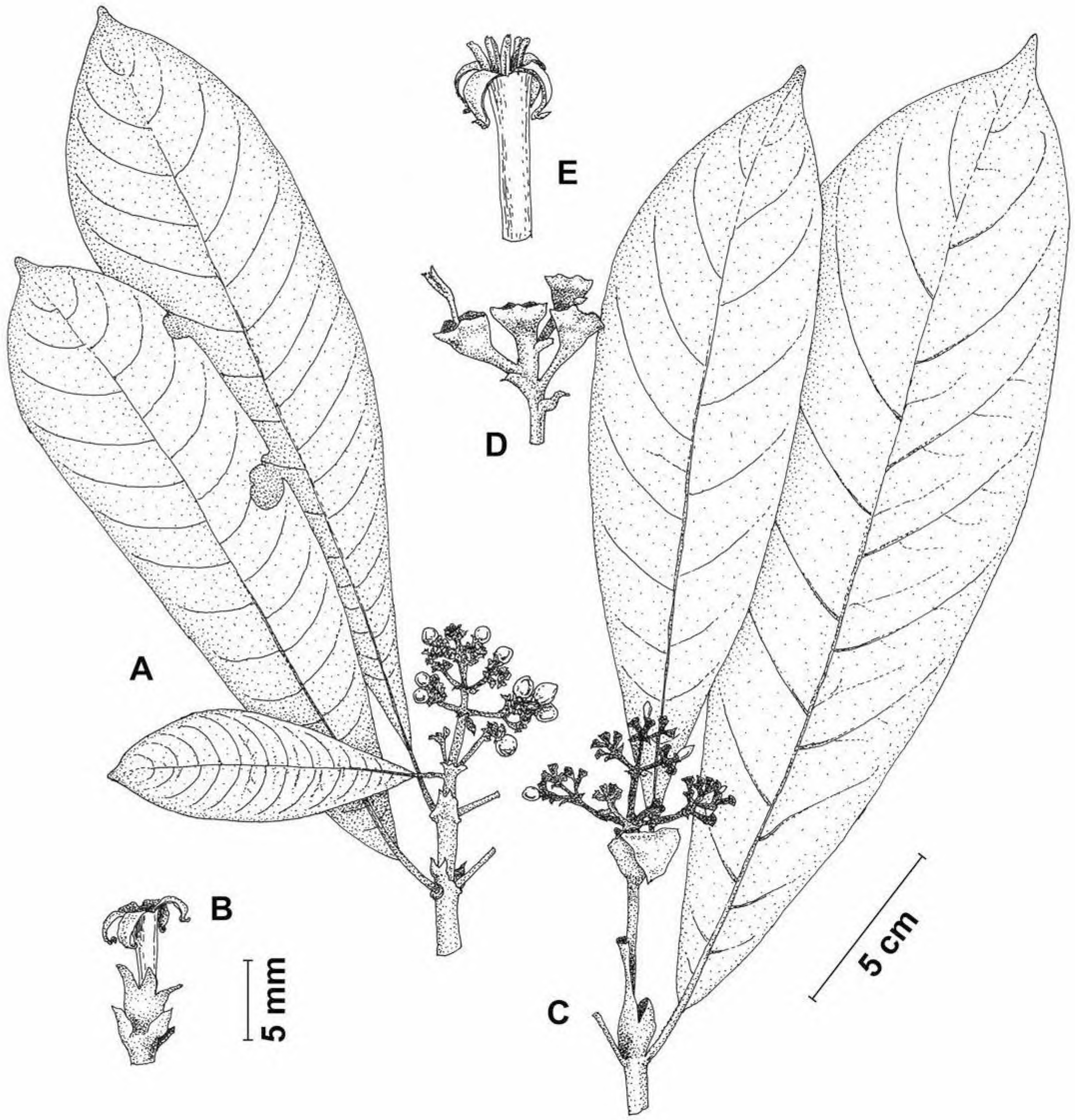


Figure 6. A, B. *Gaertnera malcomberiana* C. M. Taylor. —A. Fruiting branch; based on *Lewis 1318* (MO). —B. Portion of inflorescence with one flower at anthesis; based on the type *J. Tosh et al. 383* (MO). C–E. *Gaertnera rubra* C. M. Taylor; based on the type *L. M. Randrianjanaka 214* (MO). —C. Flowering branch. —D. Portion of inflorescence with four flowers from which corollas have fallen, one flower with persistent style with stigmas. —E. Corolla at anthesis, dissected off flower. A, C, to same 5-cm scale; B, D, E, to same 5-mm scale.

incision, complete apex not seen. Inflorescence congested cymose, many-flowered (50+), terminal on principal branches, erect, strigillose or lanose-strigose to glabrous, subsessile to pedunculate, peduncles to 0.8 cm; branched portion broadly pyramidal to corymbiform, 3.8–6 × 3.8–6 cm, branched to 2 to 4 orders; bracts narrowly triangular, 6–8 mm; bracteoles triangular, 3–4 mm, often fused to base or lower part of calyx; pedicels to 1 mm. Flowers mixed subsessile and pedicellate, with biology unknown, 5-merous; calyx cupuliform, 2.5–3 mm wide, externally glabrous, internally glabrous except strigillose in a ring near middle, tube 2.5–4 mm, lobed, lobes 5, narrowly triangular, 1.5–2.5 mm, subequal to a little unequal; corolla in bud obtuse, at anthesis salverform, white in basal part and pink above, externally glabrous, internally not seen, tube ca. 8.5 mm, cylindrical, ca. 1 mm diam. near middle, lobes triangular, ca. 2 mm, at apex abaxially with appendage ca. 0.1 mm, adaxially smooth; anthers and stigmas not seen. Drupes ellipsoid to ovoid and weakly laterally flattened with apex sometimes shortly rostrate, 7–8 × 8–9 mm, violet; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera malcomberiana* is known from subhumid forests at 1006–1630 m in the provinces of Antsiranana (SAVA) and Mahajunga (Sofia). *Gaertnera malcomberiana* has been collected in flower in February and in fruit in November.

IUCN Red List category. Although *Gaertnera malcomberiana* is present in the protected areas of Anjanaharibe-Sud and Marojejy, other subpopulations outside of the protected areas are expected to undergo population decline because of habitat degradation and conversion. Therefore, with a restricted geographic range size (EOO = 1449 km²; AOO = 930 km²) and only seven locations, *G. malcomberiana* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera malcomberiana* is similar to and has been confused previously with *G. ianthina*, which is also found in northern Madagascar; *G. ianthina* can be separated by its elliptic to oblong leaves that abaxially have strigose to sericeous pubescence along the principal veins. In contrast, the characteristic pubescence of *G. malcomberiana* is unlike that of any other *Gaertnera* species seen. This pubescence resembles arachnoid pubescence, but the matted, tangled, long (to 1.5 mm), appressed trichomes are straight to crisped. These trichomes are sometimes deciduous and/or sometimes mixed with much shorter trichomes. *Gaertnera malcomberiana* is also unusual in its often ternate leaf arrangement, which is uncommon in the genus. The specific epithet of this exceptional species honors Simon Malcomber who has studied *Gaertnera* extensively across its entire range and in particular in Madagascar.

Paratypes. MADAGASCAR. **Antisiranana:** SAVA, limite entre Anjialavabe et Doany, Andapa, sommet d'Ankarangameloka, *D. Ravelonarivo, M. Patroide & German 1852* (MO, TAN); Andapa, Ambodiangezoka, Réserve Spéciale Anjanaharibe-Sud, Quartier Antsavokabe, 11 km WSW Befingotra, 14°45′S, 49°27′E, *B. Lewis, J. McDonagh & R. Desire 1318* (K, MO, P, TAN); Réserve Naturelle Intégrale no. 12 de Marojejy, 11 km NW de village Manantenina, le long d'un affluent de la rivière Manantenina, 14°26′S, 49°44′E, *P. J. Rakotomalaza, N. Messmer & D. Ravelonarivo 809* (K, MO, P, TAN); Andranotsarabe, Befingotra, Belampona, 14°42′S, 49°32′E, *F. Rasoavimbahoaka & J. A. Rastefanonirina 311* (K, MO, P, TAN), environs du sommet, 14°42′S, 49°28′E, *D. Ravelonarivo et al. 303* (MO, P, TAN), ca. 8 km près du village d'Antsavokabe, 14°40′S, 49°30′E, *D. Ravelanarivo & M. Rabarisoamanana 912* (MO, P, TAN); Réserve Spéciale Anjanaharibe-Sud, village d'Andranotsarabe, 14°45′S, 49°28′E, *D. Ravelonarivo & R. Rabesonina 499* (K, MO, P, TAN), Quartier Ambodisatrana, SW d'Andapa, au bord de la rivière Beamalona, 14°39′S, 49°26′E, *D. Ravelonarivo & R. Rabesonina 685* (MO, P, TAN); Andapa, Doany, Andranomilolo, forêt d'Andrakengy, 14°20′S, 49°18′E, *R. Razakamalala, C. Rakotovao, Landrie & José 2913* (K, MO, P, TAN). **Mahajunga:** Sofia, versant O de la Réserve Spéciale Anjanaharibe-Sud, 13 km SW de Beginotra, 14°46′S, 49°26′E, *P. J. Rakotomalaza & D. Ravelomanantsoa 2100* (G, MO, TAN).

24. Gaertnera masoalana C. M. Taylor, sp. nov. TYPE: Madagascar. Antsiranana: SAVA, Masaola Peninsula, 0–1 km NW of "Tamany Rabe Pierre" watershed of Anaovandrano River, 15°44′S, 50°13′E, 50 m, 16 Nov. 1996, *G. E. Schatz, J. Dransfield, S. Dransfield & R. Bernard 3683* (holotype, MO-6023166!; isotypes, K n. v., P n. v., TAN n. v.). Figure 5A–C.

Haec species a *Gaertnera phanerophlebia* Baker foliis plerumque domatiis praeditis, inflorescentia sessili usque pedunculata cymosa duplo vel triplo ramificante atque lobis calycinis 1.5–5 mm longis distinguitur.

Shrubs and small trees to 10 m tall, drying orangish brown to brown; branchlets 1.5–3.5 mm diam., quadrangular to a little flattened, hirtellous to glabrous. Leaves opposite; blades oblanceolate to narrowly elliptic, 7–13 × 1.5–5 cm, drying chartaceous to subcoriaceous and matte, adaxially glabrous, abaxially glabrous or hirtellous on midrib and sometimes also secondary veins, at base acute to cuneate, at apex acute to acuminate with tips 3–10 mm; secondary veins 9 to 12 pairs, abaxially prominent, usually with foveolate and sometimes also hirtellous domatia 0.2–0.5 mm diam., with tertiary venation not evident or sometimes weakly visible abaxially; petioles 6–18 mm, hirtellous to glabrous; stipules calyptrate, hirtellous to glabrous, drying membranaceous and reddish brown, deciduous via fragmentation, tube 10–22 mm, smooth or weakly ridged, with rounded to flat wings 0.5–1.5 mm wide encircling petioles and extending to base of tube, apex with 1 incision, triangular, with 2 to 4 linear lobes 2–4 mm. Inflorescences rather densely cymose, many-flowered (50+), terminal on principal branches, erect, densely hirtellous to glabrescent, sessile to pedunculate, peduncles to 2 cm; branched portion corymbiform, 3–7 × 4–7 cm, branched to 2 to 3 orders; bracts ligulate to narrowly oblanceolate, 5–10 mm; bracteoles ligulate, 3–8 mm. Flowers sessile, distylous, 5-merous; calyx cupuliform, 2–3 mm wide, externally strigillose to glabrous, internally glabrous, tube ca. 2 mm, lobes 3 to 5, ligulate, 1.5–5 mm, subequal to unequal; corolla in bud obtuse, at anthesis salverform, white, externally glabrous to sparsely pilosulous-puberulous, internally glabrous except densely villosulous in upper part of tube, tube 3.5–5 mm, cylindrical to slightly funnelform, ca. 1 mm diam. near middle, lobes triangular, 1–1.5 mm,

at apex abaxially a little thickened, adaxially weakly hooked; anthers in long-styled form ca. 0.8 mm, partially exserted, in short-styled form ca. 1 mm, exserted; stigmas in long-styled form ca. 0.3 mm, exserted, in short-styled form ca. 1.2 mm, positioned in upper part of corolla tube. Drupes not seen.

Habitat, distribution, and phenology. *Gaertnera masoalana* is known from wet forests at 50–294 m in the provinces of Antsiranana (SAVA) and Toamasina (Analanjirofo and Atsinanana). It has been collected mainly or perhaps only on quartz outcrops. *Gaertnera masoalana* has been collected in flower from October through December and is not yet documented in fruit.

IUCN Red List category. *Gaertnera masoalana* is known only from three subpopulations in lowland humid forest, two of which are within the Masoala protected area. With a restricted geographic range size (EOO = 4794 km^2), expected decline of the subpopulation that is lacking protection at Maroseranana, and only three locations, *G. masoalana* is here considered to be Endangered [EN B1ab(iii)].

Discussion. *Gaertnera masoalana* is well documented in the area of the Masoala Peninsula, and the species epithet refers to this range. It can be recognized by the combination of its slender stems and leaves, deciduous calyptrate stipules, rather short, densely corymbiform inflorescences, calyx with generally ligulate lobes, and relatively short corollas. *Gaertnera masoalana* is similar in general aspect to *G. phanerophlebia*, which is found from northern through east-central Madagascar; *G. phanerophlebia* can be recognized by its leaves that lack domatia; subsessile, subcapitate to densely congested cymose inflorescences with the axes not evident; and larger corollas with tubes 9.5–17 mm long (for the contrasting characters of *G. masoalana*, see its description above). This new species is also similar to *G. velutina*, described later in this article and found widely through eastern Madagascar; *G. velutina* can be recognized by its tubular, generally persistent stipules, inflorescences with the flowers mixed sessile and pedicellate, and longer corollas with tubes 5–6 mm. Several specimens of *G. masoalana* were cited by Malcomber and Taylor (2009) as *G. obovata* var. *sphaerocarpa*, which is widely distributed in Madagascar; however, *G. obovata* var. *sphaerocarpa* can be separated by its calyx with the lobes only up to 1 mm long and usually shorter and distribution at generally higher elevations, 360–1876 m.

Paratypes. MADAGASCAR. **Antsiranana:** SAVA, Masoala Nat. Park, near Andranobe, 15°39′S, 49°57′E, *Moïse 4* (MO). **Toamasina:** Analanjirofo, Masoala Nat. Park, W coast, near Andranobe, 15°40′S, 49°57′E, *S. T. Malcomber 2813* (MO); Atsinanana, Brickaville, Maroseranana, N du village d'Andeka, 18°33′S, 48°51′E, *T. Andriamihajarivo, R. Razakamalala, J. L. Andriatiana & J. Samisy 703* (MO).

25. Gaertnera microphylla Capuron ex Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 390, figs. 2, 6. 2005. TYPE: Madagascar. Toamasina: Alaotra-Mangoro, 6.6 km SE of Andasibe, small ridge beside RN2 at base of Andriandavibe, 23 Nov. 1997, *S. T. Malcomber, A. Davis, D. Gower & J. Andriantiana 2925* (holotype, MO; isotypes, A, BR, G, K, LE, MAL, MAU, P, PRE, TEF, UPS, WAG).

Distribution and IUCN Red List category. *Gaertnera microphylla* is found in central eastern Madagascar at 790–1050 m in the province of Toamasina. Although this species is present in the protected areas of Analamazaotra-Périnet and Mantadia, it has an extremely restricted geographic range size (EOO ca. 100 km^2; AOO ca. 60 km^2) in subhumid forest only in the Périnet–Mantadia region. Given continuing decline outside of these protected areas due to habitat degradation and conversion and its only four known locations, *G. microphylla* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

See Malcomber and Taylor (2009: 635–636) for a species description.

26. Gaertnera monstruosa Malcomber, Ann. Missouri Bot. Gard. 96(4): 636, fig. 12A–D. 2009. TYPE: Madagascar. Toamasina: Analanjirofo, 6.4 km W of Antanambe, Mananara Nat. Park, lowland rainforest, 180 m, 16 Nov. 1997, *S. T. Malcomber 2887* (holotype, MO; isotypes, BR, K, P, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera monstruosa* is found in northeastern Madagascar in the provinces of Toamasina and Fianarantsoa at 50–570 m. It is distributed in humid forest from west of Foulepointe at Analalava to northwest of Maroantsetra and is present in the protected areas of Ambatovaky, Makira, and Mananara-Nord as well as the conservation site Analalava. With a restricted geographic range size (EOO = 8396 km^2; AOO ca. 4000 km^2), expected continuing decline outside of protected areas due to habitat degradation and conversion, and only five known locations, *G. monstruosa* is here considered to be Vulnerable [VU B1ab(iii)].

See Malcomber and Taylor (2009: 636–637) for a species description.

27. Gaertnera nitida C. M. Taylor, sp. nov. TYPE: Madagascar. Antsiranana: DIANA, Presqu'île

d'Ampasindava, forêt de Bongomihiravavy, 13°45′55″S, 48°03′08″E, 278 m, 28 Nov. 2007, *L. Nusbaumer 2585* (holotype, G!; isotype, MO-6306900!). Figure 7A, B.

Haec species a *Gaertnera obovata* var. *sphaerocarpa* (Baker) Malcomber et *G. macrostipula* Baker foliis crassis plerumque nitidis venatione subtiliter reticulata abaxialiter manifesta atque corolla breviore, etiam a hac stipulis tubularis distinguitur.

Shrubs to 10 m tall, drying greenish brown or brown; branchlets 3–5 mm diam., flattened, glabrous. Leaves opposite; blades obovate, oblanceolate, elliptic, or elliptic-obovate, 6–15 × 3.5–9 cm, drying chartaceous to subcoriaceous and shiny, glabrous on both surfaces, at base obtuse to cuneate, at apex obtuse to rounded or truncate and sometimes abruptly acuminate with tips 1–5 mm; secondary veins in 4 to 6 pairs, plane to thinly prominulous abaxially, with foveolate domatia 0.3–0.5 mm diam., with intersecondary and tertiary venation extensively reticulated and visible abaxially; petioles 10–30 mm, glabrous; stipules tubular, glabrous, drying papery and dark brown, generally persistent, tube 15–25 mm, smooth, wings absent or tardily developing, rounded, ca. 0.5 mm, encircling bases of petioles, apex with 1 or 2 incisions, with 2 triangular lobes 1–2 mm. Inflorescence rather congested to rather laxly cymose, many-flowered (50+), terminal on principal branches, erect, sparsely to densely pilosulous-puberulous, pedunculate; peduncle 0.8–3.5 cm; branched portion pyramidal to corymbiform, 3–16 × 6–14 cm, branched to 3 to 4 orders; bracts ovate to narrowly triangular, 2–35 mm; bracteoles ovate to triangular, 1–5 mm. Flowers sessile or subsessile, distylous, 5-merous; calyx cupuliform, 2.2–3 mm wide, internally and externally glabrous, tube 1.8–3 mm, truncate to lobed, lobes 5, broadly to narrowly triangular, 0.5–2 mm, subequal to unequal; corolla in bud obtuse to acute, at anthesis salverform, white, externally glabrous, internally densely barbate on upper part of tube and onto bases of lobes, tube 3–5 mm, cylindrical to funnelform, 1–1.5 mm diam. near middle, lobes ligulate, 2–3 mm, at apex abaxially smooth or a little thickened, adaxially hooked; anthers in long-styled form ca. 2 mm, partially exserted, in short-styled form ca. 1.5 mm, exserted; stigmas in long-styled form 1–1.2 mm, well exserted, in short-styled form ca. 1.2 mm, positioned in upper part of corolla tube. Immature drupes ovoid, 6–7 mm diam.; pyrenes 2, hemispherical, abaxially smooth.

Habitat, distribution, and phenology. *Gaertnera nitida* is known from subhumid to dry vegetation, often on sandy substrates at 50–350 m in northwestern Madagascar in the provinces of Antisranana (DIANA) and Mahajunga (Sofia). *Gaertnera nitida* has been collected in flower in August, September, October, and November and in fruit in February through April.

IUCN Red List category. *Gaertnera nitida* is present in the protected areas of Ankarafantsika and Manongarivo. With a restricted geographic range size (EOO = 13,133 km²; AOO ca. 1200 km²), expected continuing decline outside of protected areas due to habitat degradation and conversion, and 13 known locations, *G. nitida* is here considered to be Near Threatened (NT).

Discussion. *Gaertnera nitida* extends into the dryest habitats of any species of *Gaertnera*, and can be recognized by its stiff, generally shiny leaves with regularly developed domatia and the finely reticulated tertiary venation visible on the lower surface, persistent smooth stipule tubes, and rather short corollas. The species epithet refers to the leaves, which are often shiny on both upper and lower surfaces. *Gaertnera nitida* as circumscribed here includes some morphological variation in the length of the bracts, the shape and size of the bracteoles, and calyx form. The specimen *Malcomber & Rakotomalala 2594* and the type specimen have well-developed inflorescence bracts up to 20 mm long, relatively long bracteoles, and relatively long calyx lobes. Most of the other specimens studied have short bracts and bracteoles and a truncate to denticulate calyx, but several specimens are intermediate in form. For example, *Cheek 2190* has well-developed bracts with the largest ones 15–35 mm long, ovate bracteoles 1–2 mm long, and triangular calyx lobes 0.8–1 mm, while *Service Forestier 7680* has relatively short bracts and bracteoles but long calyx lobes ca. 0.8 mm long.

Gaertnera nitida was previously confused with *G. obovata* var. *sphaerocarpa*, which is found widely in Madagascar, but *G. obovata* var. *sphaerocarpa* differs in its thinner textured leaves with the lower surface not shiny, quickly caducous stipules, and habitat generally in humid forest predominantly above 800 m elevation (for the contrasting characters of *G. nitida*, see its description above). *Gaertnera nitida* was also previously confused with *G. macrostipula*, which is also found widely in Madagascar; *G. macrostipula* can be recognized by its tubular, usually inflated stipules, leaves that are not shiny and have the tertiary venation sparsely or not at all visible, and longer corollas with tubes 6.5–9 mm long. *Gaertnera nitida* is also similar to *G. sclerophylla* and *G. breviflora*; see the discussion of *G. sclerophylla* for the separation of

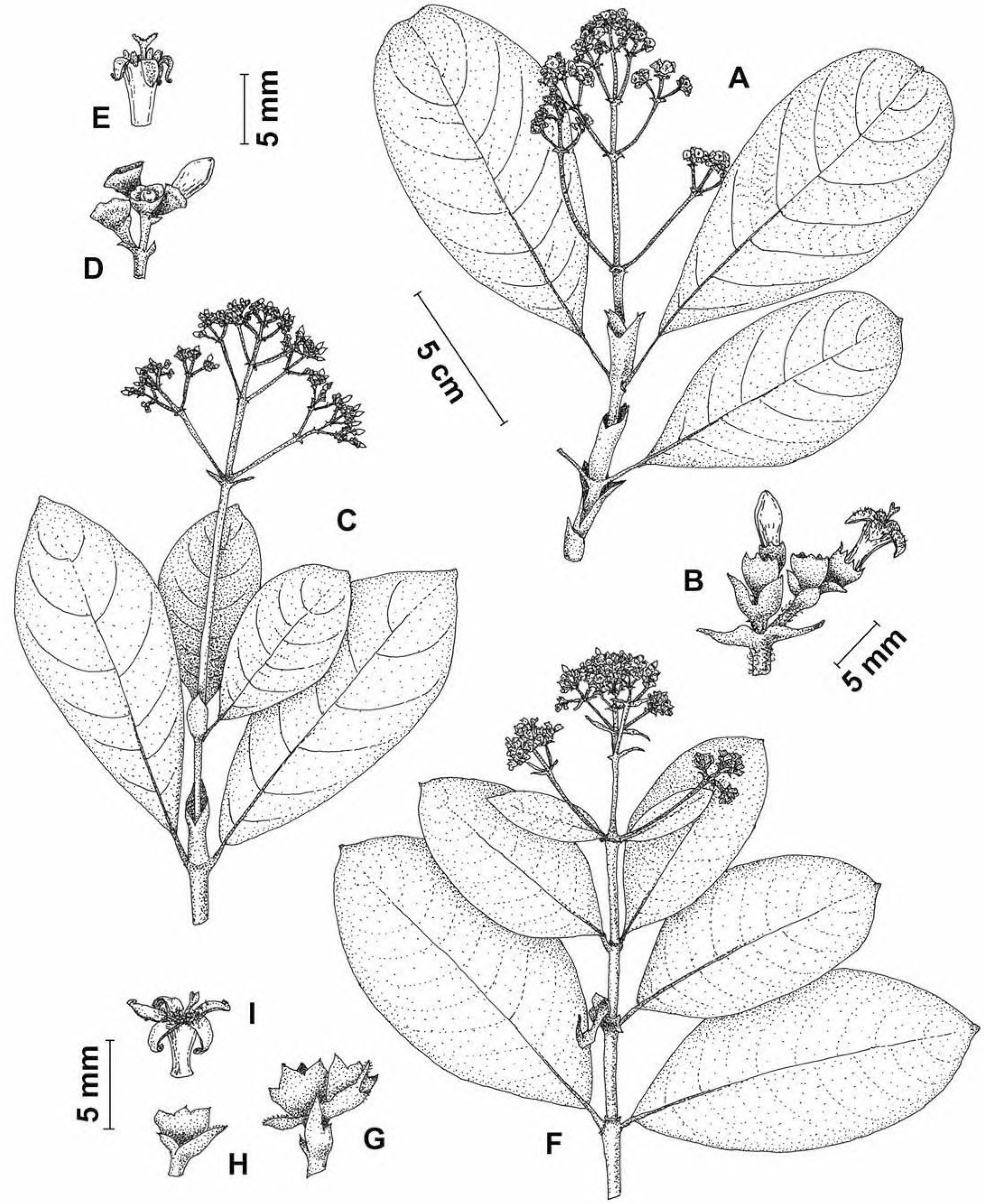


Figure 7. A, B. *Gaertnera nitida* C. M. Taylor. —A. Flowering branch; based on *S. Wohlhauser et al. 734* (MO). —B. Portion of inflorescence with one flower bud, one flower at anthesis, and two flowers from which corollas have fallen, based on *L. Gautier & P. Derlith 2514* (MO). C–E. *Gaertnera sclerophylla* C. M. Taylor; based on the type *G. McPherson & J. Rabenantoandro 18404* (MO). —C. Flowering branch. —D. Portion of inflorescence with one flower bud and three flowers from which corollas have fallen. —E. Corolla at anthesis, with style, dissected off flower. F–I. *Gaertnera xerophila* C. M. Taylor; based on the type *D. Rabehevitra et al. 410* (MO). —F. Flowering branch. —G. Portion of inflorescence with two flowers from which corollas have fallen. —H. Flower from which the corolla has been removed. —I. Corolla at anthesis, dissected off flower, together with style. A, C, F, to same 5-cm scale; G–I, to same 5-mm scale.

these and several other species found in littoral vegetation. *Gaertnera nitida* is also similar to *G. vernicosa*; for their separation see the discussion under *G. vernicosa*.

Paratypes. MADAGASCAR. **Antsiranana:** DIANA, sud d'Ambilobé, *R. Decary 14790* (MO); Montagne d'Ambato, 13°26′S, 48°33′E, *J. Kårehed, S. Razafimandimbison & H. Bremer 253* (MO, UPS), Ambilobe, Beramanja, Ankazomahitsy, Savoka à Ravinala, 13°28′S, 48°44′E, *R. Ludovic 26* (MO), Ampasindava, forêt de Bongomihiraravy, *L. Nusbaumer, P. Ranirison, M. C. Madiomanana, N. Y. Ammann, D. J. Tahinanarivony & R. Bernard 2733* (G, MO); Ambilobe, Beramanja, forêt de Kalabenonon, sur la chaine Galoko, 7 km SE d'Anketrabe, 13°38′S, 48°40′E, *J. Razafitsalama, Torze & E. Toninjama 1031* (K, MO), Ambilobe, Beramanja, Chaîne Galoka, Mont Galoka, Anketrabe-Belinta, 13°35′S, 48°43′E, *S. Wohlhauser, Tonga, M. S. Ravokatra, A. Lang, N. Manasse, C. Claude & G. Bocksberger 734* (MO); presqu'île d'Ampasindava, forêt de Andranomatavy, 13°40′13″E, 47°59′07″S, *M. Y. Ammann, M. C. Madiomanana & A. J. Tahinarivony 367* (K, G, MO); Ambanja, Ambaliha, Tsarabanja, forêt d'Ambohimirahavy, *R. Bernard, Louis, Patrick, Jacky, Cathy, Morgane, Ndrianary & Pierre 1204* (MO, TAN); Ambanja, Bemanevika, Bandrakorony, forêt de Bandrakorony, 13°45′35″S, 47°59′26″E, *R. Bernard et al. [no other collectors listed] 1242* (G, MO); forêt du côté Ouest de la grande rivière de Bandrakorony sur la Péninsula d'Ampasindava, 13°44′49″S, 47°59′36″E, *C. Rakotovao, Maevalignitry & Zazà 4165* (G, MO), *4267* (G, MO), Ambanja, village Beampongy, *Service Forestier de Madagascar 7680* (MO); Réserve Spéciale de Manongarivo, Besinkara, Ambalafary, 14°04′S, 48°17′E, 350 m, *L. Gautier & P. Derlith 2514* (K, G, MO), E of Ankarakmy Be Manongarivo Reserve Special, Bekolosy, 14°03′S, 48°17′E, *S. T. Malcomber & L. Rakotomalala 2594* (K, MO); Antanambao, contreforts occidentaux de la plaine du Sambirano, Maevatanana, 13°55′S, 48°30′E, *S. Wohlhauser & H. Andriamalaza 60225* (G, MO). **Mahajunga:** Sofia, Maromandia, Antsohihy, 22 km, 14°12′S, 48°08′E, *M. Cheek, A. Rakotozafy & Raharilala 2190* (K, MO); RN7, Marovoay, *Reserves Naturelles de Madagascar 6653RN* (MO).

28. Gaertnera obovata Baker, J. Bot. 20: 218. 1882. *Sykesia obovata* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. "Chiefly from Betsileo-land," *R. Baron 149* (holotype, K; isotype, P).

Distribution and IUCN Red List category. *Gaertnera obovata* is found from northwestern to eastern and southeastern Madagascar at 0–850 m, in the provinces of Mahajunga, Antsiranana, Toamasina, Fianarantsoa, and Toliara. With a large geographic range size (EOO = 358,800 km^2) and a presence in numerous protected areas (Analamazaotra-Perinet, Andohahela, Andringitra, Anjanaharibe-Sud, Betampona, Isalo, Ivohibe, Makira, Manongarivo, Mantadia, Marojejy, Masoala, Ranomafana, Tsaratanana, and Zahamena), *G. obovata* is here considered to be of Least Concern (LC).

Discussion. Two varieties of *Gaertnera obovata* were recognized by Malcomber and Taylor (2009: 639–641); see that work and couplet #40 of the Key to Species here for their distinction. Here *G. obovata* var. *obovata* is circumscribed following Malcomber and Taylor (2009), but *G. obovata* var. *sphaerocarpa* is circumscribed more narrowly. Several of the specimens included in *G. obovata* var. *sphaerocarpa* by Malcomber and Taylor (2009) are classified here into several newly described species, and accordingly a revised description is presented here.

28a. Gaertnera obovata Baker var. **obovata.**

Distribution and IUCN Red List category. This variety is found from northwestern to eastern and southeastern Madagascar at 10–2000 m, in the provinces of Mahajanga, Antsiranana, Toamasina, and Fianarantsoa. With a large geographic range size (EOO = 208,917 km^2) and a presence in numerous protected areas (Andohahela, Andringitra, Anjanaharibe-Sud, Ivohibe, Makira, Manongarivo, Mantadia, Marojejy, Masoala, Ranomafana, Tsaratanana, and Zahamena), *Gaertnera obovata* var. *obovata* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 639–640) for a description of this variety.

28b. Gaertnera obovata var. **sphaerocarpa** (Baker) Malcomber, Ann. Missouri Bot. Gard. 96(4): 640, fig. 13G–L. 2009. *Gaertnera sphaerocarpa* Baker, J. Linn. Soc. Bot. 20: 208. 1883. *Sykesia sphaerocarpa* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. Central Madagascar, *R. Baron 1243* (lectotype, designated by Malcomber & Taylor [2009: 640], K; isotype, P).

Shrubs or small trees to 7 m tall, drying greenish brown; branchlets 2.5–5 mm diam., quadrangular, glabrous, sparsely hirtellous, or sparsely to densely pilosulous. Leaves opposite; blades obovate or oblanceolate, 6–23.5 × 1.8–9 cm, drying chartaceous and matte, glabrous throughout or abaxially sparsely hirtellous to densely pilosulous on principal veins, at base acute to cuneate, at apex obtuse to rounded or truncate and usually abruptly acuminate with tips 2–5 mm; secondary veins in 5 to 11 pairs, abaxially prominulous, with pilosulous domatia, with secondary, intersecondary, and tertiary venation generally visible abaxially; petioles 3–22 mm, glabrous or sparsely to densely hirtellous or pilosulous; stipules calyptrate, glabrous or sparsely hirtellous or pilosulous at least in in apical portion, drying membrana-

ceous and dark brown to reddish brown, caducous, sometimes fragmenting, 8–35 mm, smooth, with wings reduced or usually flattened to rounded, 0.2–0.5 mm, enclosing bottom and sometimes also sides of petioles, apex with 1 slit, with 2 linear teeth 2–4 mm, densely pilosulous. Inflorescence somewhat congested to laxly cymose, many-flowered (30+), terminal on principal branches, erect to perhaps deflexed, sparsely to moderately pilosulous or puberulous often in patches, pedunculate; peduncles 1–4.5 cm; branched portion broadly pyramidal to rounded-corymbiform, 2–13 × 4–18 cm, branched to 3 to 5 orders; bracts triangular to narrowly triangular, 1.5–8 mm, or occasionally those subtending secondary and sometimes tertiary axes foliaceous; bracteoles ligulate to ovate, 1–2 mm; pedicels to 2 mm. Flowers sessile or sometimes mixed sessile and pedicellate, distylous, 5-merous; calyx cupuliform, 2–3 mm wide, glabrous to puberulous or pilosulous externally, internally glabrous or usually with puberulous to strigillose ring near middle or base, tube 1.5–2 mm, denticulate to dentate, teeth 5, triangular, 0.1–1 mm, equal or subequal; corolla obtuse to truncate in bud, at anthesis salverform, white often flushed with violet or pink, externally glabrous, internally glabrous except densely barbate in upper part of tube and throat, tube 4–8 mm, cylindrical to weakly funnelform, 1.2–2 mm diam. near middle, lobes narrowly triangular, 2–3 mm, at apex abaxially thickened, adaxially shortly hooked; anthers in short-styled form ca. 1.8 mm, exserted, in long-styled form 1.8–2.2 mm, exserted; stigmas in short-styled form 1–2 mm, included, positioned near middle of corolla tube, in long-styled form 0.8–1 mm, partially to fully through shortly exserted. Drupes subglobose, 6–7 mm diam., violet to blue-black or occasionally perhaps white; pyrenes 2, hemispherical, smooth abaxially.

Distribution and IUCN Red List category. *Gaertnera obovata* var. *sphaerocarpa* is found from northwestern to eastern and southeastern Madagascar at 0–1730 m, in the provinces of Antsiranana, Toamasina, Fianarantsoa, and Toliara. With a large geographic range size (EOO = 327,035 km^2) and a presence in numerous protected areas (Analamazaotra-Périnet, Andohahela, Andringitra, Anjanaharibe-Sud, Betampona, Isalo, Ivohibe, Makira, Manongarivo, Mantadia, Marojejy, Masoala, Ranomafana, Tsaratanana, and Zahamena), *G. obovata* var. *sphaerocarpa* is here considered to be of Least Concern (LC).

Discussion. See Malcomber and Taylor (2009: 640) for synonymy. This variety can be recognized by the combination of its thin-textured, caducous, calyptrate stipules; chartaceous, oblanceolate or obovate leaves with the secondary, intersecondary, and tertiary venation regularly visible and with pilosulous domatia regularly developed; cymose inflorescences with the flowers generally sessile in dichasia; rather small, generally white corollas; and fruits 6–7 mm in diameter. The fruits are generally violet to blue-black, but occasionally reportedly white at maturity. White mature fruits are uncommon in *Gaertnera* and this may be an error in observation; however, there are species of Rubiaceae with normally blue fruits that occasionally produce white or perhaps albino fruits (e.g., *Psychotria deflexa* DC., Taylor et al., 2004; *Gonzalagunia panamensis* (Cav.) K. Schum., Taylor, 2012) and *G. obovata* var. *sphaerocarpa* may be another. As circumscribed here this variety has a range in humid forest at and above 360 m elevation, predominantly above 800 m elevation. The illustration of *G. obovata* var. *sphaerocarpa* presented by Malcomber and Taylor (2009: 640, fig. 13G–L) depicts a specimen, *Malcomber 2916*, that is here included in the newly described species *G. sclerophylla*.

Gaertnera obovata var. *sphaerocarpa* is similar to several *Gaertnera* species that are found at lower elevations and in particular *G. guillotii*, which is found along nearly the entire east coast of Madagascar; *G. guillotii* can be recognized by its generally smaller elliptic-oblong to elliptic-oblanceolate leaves, 1.7–13.2 × 0.7–4.6 cm, with the tertiary venation generally not visible; generally smaller inflorescences, with the branched portion 0.6–7 × 0.8–6.2 cm; generally smaller corollas with tubes 3–5 mm long; generally smaller fruits, 4.5–5.5 mm in diameter; and distribution in littoral forests at 0–750 m elevation (for contrasting characters of *G. obovata* var. *sphaerocarpa*, see its description above). *Gaertnera obovata* var. *sphaerocarpa* is also similar to *G. arenaria*, which is widely distributed in Madagascar; however, *G. arenaria* can be recognized by its tubular stipules with four longitudinal ribs and larger corollas with tubes 10–16 mm long. *Gaertnera obovata* var. *sphaerocarpa* is also similar to *G. sclerophylla* and *G. xerophila*; their separation is outlined in the dicussion of *G. sclerophylla*.

Representative specimens. MADAGASCAR. **Antananarivo:** Analamanga, 5.7 km ESE of Anjozorobe, 18°23′55″S, 47°56′09″E, *S. T. Malcomber, A. P. Davis & D. Gower 2836* (MO, TEF). **Antsiranana:** SAVA, E of Andapa, Marojejy Nat. Reserve, near summit of Marojejy Est, 14°26′43″S, 49°44′11″E, *S. T. Malcomber 2776* (MO, P, TEF). **Fianarantsoa:** Haute Matsiatra, Ranomafana Nat. Park, Vohiparara, 21°14′25″S, 047°23′38″E, *S. T. Malcomber, A. P. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2857* (MO, TEF). **Toamasina:** Alaotra-Mangoro,

near Andasibe, Mantadia Nat. Park, 18°49′04″S, 048°25′59″E, *S. T. Malcomber, A. P. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2917* (MO). **Toliara:** Anosy, Beampingaratra Massif, Maloto Valley, *J.-H. Humbert 6322* (MO, P).

29. Gaertnera pauciflora Malcomber & A. P. Davis, Monogr. Syst. Bot. Missouri Bot. Gard. 104: 392, figs. 5, 7. 2005. TYPE: Madagascar. Antsiranana: SAVA, E of Andapa, Marojejy Nat. Reserve, 19–20 Sep. 1997, *S. T. Malcomber 2781* (holotype, MO; isotypes, A, BR, G, K, LE, MAL, MAU, P, PRE, TEF, WAG).

Distribution and IUCN Red List category. *Gaertnera pauciflora* is found in northeastern and southeastern Madagascar, in the provinces of Antsiranana, Toamasina, and Fianarantsoa at 300–1600 m. It is widely distributed in humid to subhumid forest from Vondrozo to the Ankarongameloka forest NW of Doany. Although it is present in the protected areas of Makira and Marojejy, population decline is projected in populations outside of protected areas due to habitat degradation and conversion. With a geographic range size exceeding the threshold values for threatened status (EOO = 27,918 km²; AOO ca. 15,000 km²) and the possibility that several of the 10 currently known subpopulations may disappear in the future, *G. pauciflora* is here considered to be Near Threatened (NT).

See Malcomber and Taylor (2009: 642–643) for a species description.

30. Gaertnera phanerophlebia Baker, J. Linn. Soc., Bot. 21: 425. 1885. *Sykesia phanerophlebia* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. "Central Madagascar," *R. Baron 2982* (lectotype, designated by Malcomber & Taylor [2009: 643], K; isotypes, BM, P). Figure 3E, F.

Shrubs or small trees to 8 m tall, drying reddish brown; branchlets 2–3 mm diam., flattened to angled, glabrous or usually hirtellous to hirsute later becoming glabrescent, trichomes drying reddish brown. Leaves opposite; blades narrowly elliptic to elliptic-oblong, 3–12(14.5) × 1.4–3.5(4.5) cm, drying chartaceous and matte, adaxially glabrous except usually densely strigose or sericeous to hirsute on midrib, abaxially glabrous except usually densely sericeous, hirsute, or hirtellous on principal veins and densely ciliate on margins, at base rounded to truncate, at apex acute to shortly acuminate with tips 1–5 mm; secondary veins in 6 to 15 pairs, abaxially prominulous, without domatia, with tertiary veins not visible abaxially; petioles 2–10 mm, glabrous to densely hirtellous or hirsute; stipules calyptrate, glabrous to hirsute, drying membranceous and reddish brown, caducous or usually deciduous through fragmentation, 10–32 mm, smooth, with flattened ridges 0.2–0.5 mm wide developed below petioles and occasionally extending onto basal portion of stipule, apex usually with 1 incision, broadly triangular, 1–2 mm. Inflorescences capitate to congested cymose, many-flowered (40+), terminal on principal branches, erect, densely hirsute or hirtellous to glabrous, subsessile to pedunculate, peduncle to 0.5 cm; head or branched portion subglobose to corymbiform, 1.5–4 × 2–5 cm, unbranched or branched to 1 to 3 orders; bracts narrowly triangular, 6–10 mm; bracteoles triangular, 4–9 mm, usually fused to base of calyx or inserted shortly above base. Flowers subsessile to sessile, distylous, 5-merous; calyx cupuliform, 2–2.5 mm wide, externally villosulous or hirtellous to glabrous, internally glabrous, tube 2.5–3.5 mm, lobed, lobes 5, narrowly triangular, 2.5–6 mm, subequal or unequal with 1 or 2 lobes half as long as longest lobe; corolla in bud obtuse, at anthesis salverform, white to violet, externally glabrous to hirtellous in upper 1/2–3/4, internally puberulous to villosulous in upper half of tube and onto bases of lobes, tube 9–11.5 mm, cylindrical, 1–1.5 mm diam. near middle, lobes narrowly triangular, ca. 3 mm, at apex abaxially smooth, adaxially with short hook; anthers in long-styled form 2–2.5 mm, exserted, in short-styled form ca. 2 mm, included, positioned near middle of corolla tube; stigmas in long-styled form ca. 2 mm, exserted, in short-styled form ca. 2.5 mm, included, positioned just above middle of corolla tube. Drupes subglobose to ovoid, ca. 7 × 6 mm, mature color either green or unknown; pyrenes 2, hemispherical, smooth abaxially.

Distribution, habitat, and phenology. *Gaertnera phanerophlebia* is known from northern to east-central Madagascar in humid to subhumid forests at 33–1350 m, in the provinces of Antsiranana and Toamasina. *Gaertnera phanerophlebia* has been collected in flower in January and October through December and in fruit in March.

IUCN Red List category. With a large geographic range size (EOO = 74,561 km²; AOO ca. 22,500 km²) and its presence in numerous protected areas (Ambatovaky, Anjanaharibe-Sud, Betampona, Manongarivo, Marojejy, Masoala, and Zahamena), *Gaertnera phanerophlebia* is here considered to be of Least Concern (LC).

Discussion. As circumscribed previously this species included some plants here separated as *Gaertnera hirsuta*, as discussed in more detail under that species above. Accordingly a revised description

and illustration (Fig. 3E, F) are presented here for *G. phanerophlebia*. The specimen illustrated by Malcomber and Taylor (2009: 623, fig. 11G–M) as *G. phanerophlebia* is here included in *G. hirsuta*. See Malcomber and Taylor (2009: 643–644) for synonymy, which is not altered by the revised circumscription of this species. Davis et al. (2011) added a synonym for *G. phanerophlebia*, *Mussaenda gerrardii* Homolle.

Gaertnera phanerophlebia has been confused with *G. hirsuta*, which is found in the area of the Masoala Peninsula; *G. hirsuta* can be separated by its generally larger leaves 11.5–22 × 2.2–6.2 cm with more numerous secondary veins, 14 to 30 pairs, and the tertiary venation well developed; larger corollas with the tube ca. 11 mm and the lobes ca. 5.5 mm; and grayish green drying color (for contrasting characters of *G. phanerophlebia*, see its description above). *Gaertnera phanerophlebia* is similar in general aspect and many details to *G. hispida*, which is found from northern Madagascar to the Bay of Antongil region; *G. hispida* can be separated by its congested to rather laxly cymose inflorescences, bracteoles that are reduced or lacking, calyx limb that is truncate or has lobes only to 1.5 mm long, stouter corolla tubes 1.5–3.5 mm in diameter, and apparently larger fruits, 8–14 mm long (however, the mature fruits of *G. phanerophlebia* are not well known). *Gaertnera phanerophlebia* is also similar to *Bertiera crinita* (A. Rich.) Wittle & A. P. Davis, and these are frequently confused in sched.; *B. crinita* is found in northeastern Madagascar and can be recognized by its narrowly triangular, interpetiolar, generally persistent stipules.

There is some variation in *Gaertnera phanerophlebia* in size or robustness of the leaves and the inflorescences, and the plants are found in a variety of habitats. However, the flowers of all of these specimens are similar. This species is usually characterized in its hirsute pubescence but occasional plants are glabrous (e.g., *McPherson & van der Werff 16360*). Several specimens have the styles persistent on the young fruits, and the field notes for some collections report that the fruits seemed to be aborting (e.g., *De Block et al. 1804*, *De Block 2057* both with long-styled flowers).

Representative specimens. MADAGASCAR. **Antsiranana:** DIANA, Ambodisakoano, 14°05′S, 48°20′E, *G. McPherson & H. van der Werff 16360* (MO, TAN). **Toamasina:** Analanjirofo, Île Sainte-Marie, *L.-H. Boivin 1780* (G-DC, MO, P).

31. Gaertnera phyllosepala Baker, J. Linn. Soc., Bot. 20: 207. 1883. *Sykesia phyllosepala* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. "Central Madagascar," *R. Baron 1920* (holotype, K; isotype, P).

Distribution and IUCN Red List category. *Gaertnera phyllosepala* is known from northeastern to southeastern Madagascar, in the provinces of Antsiranana, Toamasina, Fianarantsoa, and Toliara at 0–1200 m. With a large geographic range size (EOO = 92,101 km²; AOO ca. 22,000 km²) in humid to subhumid forest and a presence in numerous protected areas (Betampona, Mananara-Nord, Masoala, Ranomafana, and Zahamena), *G. phyllosepala* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 644–646) for a species description and synonymy.

32. Gaertnera phyllostachya Baker, J. Linn. Soc., Bot. 21: 425. 1885. *Sykesia phyllostachya* (Baker) Kuntze, Revis. Gen. Pl. 2: 425. 1891. TYPE: Madagascar. s. loc., *R. Baron 2327* (lectotype, designated by Malcomber & Taylor [2009: 646], K).

Distribution and IUCN Red List category. *Gaertnera phyllostachys* is found in northeastern to southeastern Madagascar, in the provinces of Antsiranana, Toamasina, and Fianarantsoa at 100–1200 m. With a large geographic range size (EOO = 85,969 km²; AOO ca. 26,600 km²) in humid to subhumid forest and a presence in numerous protected areas (Ambatovaky, Analamazaotra-Périnet, Andringitra, Betampona, Masoala, Ranomafana, and Zahamena), *G. phyllostachys* is here considered to be of Least Concern (LC).

See Malcomber and Taylor (2009: 646–647) for a species description and synonymy.

33. Gaertnera rakotovaoana C. M. Taylor, sp. nov. TYPE: Madagascar. Antsiranana: SAVA, Andapa, Doany, à 10 km au SO d'Andranololo, Andramanalana, 14°23′S, 49°22′E, 1489 m, 28 Apr. 2006, *C. Rakotovao, D. Ravelonarivo, Rico, Landry & R. Razakamala 3101* (holotype, MO-6310162!; isotypes, P n. v., TAN n. v.). Figure 4D–F.

Haec species a *Gaertnera ianthina* Malcomber pubescentia pilosula hirtellave, foliorum venis secundariis paucioribus, bracteolis plerumque majoribus atque floribus albis distinguitur.

Shrubs to 6 m tall, drying brown to orange-brown; branchlets 3–5 mm diam., quadrangular, moderately to densely hirtellous to glabrescent. Leaves opposite; blades elliptic to oblong, 10.5–20.5 × 2–6.8 cm, drying papery to chartaceous and matte, adaxially glabrous, abaxially glabrous or hirtellous on midrib

and sometimes secondary veins, at base cuneate to obtuse, at apex acuminate with tips 5–11 mm long; secondary veins in 10 or 11 pairs, prominulous abaxially, without or usually with a few foveolate domatia ca. 0.2 mm, with intersecondary and tertiary venation not or weakly visible abaxially; petioles 3–11 mm, hirtellous or pilosulous-hirtellous to glabrescent; stipules calyptrate, moderately to densely hirtellous, drying reddish brown and membranaceous to papery, caducous, 25–28 mm, smooth or weakly 2-ribbed, with flattened wings 0.5–1.5 mm wide encircling petioles, apex with 1 incision, with 4 narrowly triangular lobes ca. 3 mm, strigillose to hirtellous, often remaining closely grouped or perhaps fused. Inflorescences laxly cymose, many-flowered (50+), terminal on principal branches, apparently erect, moderately to densely pilosulous or hirtellous-pilosulous, pedunculate; peduncle 2–6 cm; branched portion pyramidal, 9–15 × 6.5–14 cm, branched to 3 to 4 orders; bracts narrowly ligulate or narrowly triangular, 3–18 mm, or often basalmost secondary axes ebracteate or with foliaceous bracts; bracteoles ligulate to narrowly triangular, 2–5 mm; pedicels 2–5 mm. Flowers mixed sessile and pedicellate, distylous, 5-merous; calyx cupuliform, 2.5–3 mm wide, externally pilosulous-hirtellous to puberulous, internally strigillose throughout, tube 1.5–2 mm, lobed, lobes 4 or 5, triangular, 0.5–1.2 mm; corolla in bud obtuse, at anthesis salverform, white, externally glabrous on tube and hirtellous-puberulous on lobes, internally barbate on upper part of tube and lobes, tube 7.5–10 mm, cylindrical, ca. 1.2 mm diam. near middle, lobes ligulate, 3–4 mm, at apex adaxially weakly hooked, abaxially thickened; anthers in short-styled form ca. 3 mm, partially exserted, in long-styled form ca. 2 mm, included, positioned near middle of corolla tube; stigmas in short-styled form ca. 0.5 mm, exserted, apparently positioned near anthers, in long-styled form 1.2–1.5 mm, exserted. Immature drupes subglobose, to 8 mm diam.; pyrenes apparently 2.

Habitat, distribution, and phenology. *Gaertnera rakotovaoana* is known from subhumid forest in northern Madagascar at 738–1489 m in the province of Antsiranana (SAVA region). *Gaertnera rakotovaoana* has been collected in flower in February and with immature fruits in May.

IUCN Red List category. *Gaertnera rakotovaoana* is known from only six collections from the northern mountains, with an extremely restricted geographic range size (EOO = 635 km^2; AOO ca. 350 km^2). It is currently not documented from any protected areas, and is therefore expected to suffer a considerable population reduction, greater than 80%, over the next three generations (generation length estimated to be ca. 15 years). Therefore, *G. rakotovaoana* is here considered to be Critically Endangered (CR A3c).

Discussion. *Gaertnera rakotovaoana* can be recognized by its combination of pilosulous-hirtellous pubescence on the stipules, petioles, and veins of the leaf undersides, calyptrate caducous stipules, moderately large elliptic-oblong leaves, robust lax inflorescences with the individual flowers or small groups of flowers well separated, and white corollas with tubes 7.5–9 mm. The flowers are interpreted as distylous based on the documentation by specimens of flowers with two different anther positions, but are unusual in apparently having the stigmas positioned very close to the anthers in both forms. This aspect of the flowers is not well preserved on the specimens studied, but is inferred from the lengths of the styles of those flowers. The specific epithet of this handsome species honors Charles Rakotovao, collector of most of the specimens of this species as well as numerous other excellent specimens that extensively document Madagascar's flora for science.

Gaertnera rakotovaoana is similar in general aspect to *G. ianthina*, which is found in northern and northeastern Madagascar; *G. ianthina* can be recognized by its densely strigose pubescence, leaves with more numerous secondary veins, 14 to 20 pairs, mostly shorter bracteoles, 0.5–2 mm long, and pink to purple corollas. *Gaertnera rakotovaoana* is also similar to *G. hirsuta*, which is found in the Bay of Antongil region; *G. hirsuta* can be recognized by its hirsute pubescence, leaves with more numerous secondary veins, in 14 to 30 pairs, subcapitate to congested cymose inflorescences with the branched portion 4–7 cm long, larger corollas with tubes at least 11 mm long, and habitat at lower elevations, 0–600 m.

Paratypes. MADAGASCAR. **Antsiranana:** SAVA, Andapa, Ambodivohitra, forêt humide de Tsaralanto située à 12 km au SO d'Anjialavabe et au N d'Anjialavehely, 14°14′S, 49°26′E, *C. Rakotovao, J. Ihasotra & J. Rabevazaha 2707* (MO, P, TAN); Andapa, Doany, à 10 km au SO d'Andranololo, Andramanalana, 14°22′S, 49°23′E, *C. Rakotovao, D. Ravelonarivo, Rico, Landry & R. Razakamala 3204* (MO), Andranomilolo, *R. Rakotovao, R. Razakamalaza, D. Ravelonarivo, Rambimison (Ambalamasay) & José (Ambalamanasay) [sic on label] 3414* (K, MO); Anjialavahely, Antsahabalihe à 10 km vol d'ouiseau au N d'Anjialava, *D. Ravelonarivo et al. [no collectors listed] 1616* (MO, TAN); Sambava, Bevontro, Tsaratanana, à ca. 10 km SW de Morafeno, 14°11′S, 49°19′E, *C. Rakotovao, R. Razakamalaza, D. Ravelonarivo & José (Ambalamansy) [sic on label] 3583* (MO); Vohemar, Andrafainkona, forêt de Maromaniry, à 5 km au N d'Amspisarahina, 13°39′S,

49°33′E, *O. Randriambololomamonfy, R. Razakamalala & Jaowind 391* (MO).

34. Gaertnera raphaelii Malcomber, Ann. Missouri Bot. Gard. 96(4): 649, fig. 4G–I. 2009. TYPE: Madagascar. Fianarantsoa: Vatovavy-Fitovinany, Ranomafana Nat. Park, 900 m, Nov. 1991, *S. T. Malcomber et al. 1018* (holotype, MO; isotypes, BR, G, TAN, WAG).

Distribution and IUCN Red List category. *Gaertnera raphaelii* is found in east-central to southeastern Madagascar at 200–1000 m in the provinces of Fianarantsoa and Toliara. It is distributed in humid to subhumid forest from Andohahela to the Sakaleona River. This species is present in the protected areas of Andohahela, Andringitra, Ivohibe, Midongy Sud, and Ranomafana. With a geographic range size in excess of the threatened status thresholds (EOO = 23,196 km²; AOO ca. 8000 km²) and 20 locations, *G. raphaelii* is here considered to be of Least Concern (LC).

See Malcomber amd Taylor (2009: 649–650) for a species description.

35. Gaertnera razakamalalana C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Analanjirofo, Station Forestière Tampolo, 9 km N of Fenerive, 17°17′S, 49°25′E, 10 m, 25 Nov. 1994, *G. E. Schatz, L. Raholivelo, V. Rahar-imalala & J. Randriamampionona 3604* (holotype, MO-5714880!; isotypes, K n. v., P n. v., TAN n. v.). Figure 2G–I.

Haec species a *Gaertnera macrostipula* Baker inflorescentiae pedunculo plerumque breviore ac parte ramosa pyramidali, corolla breviore atque calyce subtruncato usque denticulato, a *G. obovata* var. *sphaerocarpa* (Baker) Malcomber stipulis tubularibus plerumque persistentibus distinguitur.

Shrubs and small trees to 11 m tall, drying brown or grayish brown; branchlets 5–7 mm diam., quadrangular to somewhat flattened, glabrous. Leaves opposite; blades obovate to oblanceolate, 9.5–25 × 4–10.5 cm, drying subcoriaceous and matte, glabrous on both surfaces, at base acute to cuneate or weakly obtuse, at apex rounded to truncate or shallowly retuse and infrequently then abruptly acuminate with tips 1–1.5 mm; secondary veins 7 to 9 pairs, abaxially prominulous, without domatia or sometimes with pilosulous patches deeply embedded in vein axils, with intersecondary and tertiary venation generally not visible or sometimes sparsely weakly visible abaxially; petioles 10–30 mm, glabrous; stipules tubular, glabrous, drying membranaceous to chartaceous and reddish brown to dark brown, generally persistent, smooth, tube 6–12 mm, somewhat inflated, becoming marcescent on margins, wings flattened, 0.5–1 mm, encircling petioles, apex with 2 or 4 incisions sometimes extending to base of tube, with 4 triangular teeth ca. 1 mm, glabrous to strigillose, often each tooth with ridge extending from its base downward for 1/4–1/3 of length of stipule tube. Inflorescence laxly cymose, many-flowered (50+), terminal on principal branches, erect, moderately to densely puberulous, pedunculate; peduncle 2–5 cm; branched portion pyramidal, 11–19 × 10–26 cm, branched to 4 or 5 orders; bracts narrowly triangular, 1.5–5 mm, or those subtending secondary axes sometimes foliaceous; bracteoles ligulate to broadly triangular, 0.8–1 mm; pedicels to 1 mm. Flowers sessile to subsessile or shortly pedicellate, with biology unknown, 5-merous; calyx cupuliform, ca. 2 mm wide, externally puberulous to glabrous, internally glabrous, tube 1–1.2 mm, denticulate to subtruncate, teeth 5, triangular, up to 0.2 mm; corolla obtuse to rounded in bud, at anthesis salverform, white, externally glabrous, internally densely barbate in throat, tube ca. 3 mm, funnelform, ca. 1.2 mm diam. near middle, lobes triangular to ligulate, ca. 2 mm, at apex abaxially smooth or weakly thickened, adaxially shortly hooked; anthers in presumed long-styled form ca. 2 mm, partially exserted; stigmas in presumed long-styled form ca. 0.8 mm, exserted. Drupes subglobose to ellipsoid, 6–8 × 6–8 mm, mature color unknown; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera razakamalazana* is known from littoral forests at 0–150 m in the province of Toamasina (Analanjirofo), in east-central Madagascar. *Gaertnera razakamalalana* has been collected in flower in November and in fruit in January, February, April, and May.

IUCN Red List category. *Gaertnera razakamalazana* is known from littoral forest vegetation at only three locations: the Ambohidena forest on Île Sainte Marie (Nosy Boraha), the conservation site Pointe Larrée, and the Tampolo forestry station. With a very restricted geographic range size (EOO = 1600 km²; AOO ca. 50 km²) and an expected continuing decline outside of conservation areas due to forest degradation and clearing, *G. razakamalazana* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera razakamalazana* can be recognized by its tubular, somewhat inflated, generally persistent stipules, robust leaves that are generally rounded to truncate at the apex, generally quite robust inflorescences with relatively small

bracts and bracteoles, and relatively small flowers. The inflorescences are distinctive in their peduncles that are relatively short compared to the branched portion, with the peduncle typically equal to or shorter than the first internode (i.e., section) of the primary axis of the branched portion. The stipules are also distinctive in their somewhat inflated tubes that are usually marcescent along their margins and irregularly incised. The specific epithet of this robust species honors Richard Razakamalala, collector of several specimens of this species as well as numerous other excellent specimens that extensively document Madagascar's flora for science.

Gaertnera razakamalalana is similar in general aspect to *G. obovata* var. *sphaerocarpa*, which is widely distributed in Madagascar; *G. obovata* var. *sphaerocarpa* can be recognized by its spathaceous, generally caducous stipules, leaves with the tertiary venation regularly visible abaxially, longer corollas with tubes 4–8 mm long, and distribution at higher elevations, 360–1876 m (for contrasting characters of *G. razakamalala*, see its description above). *Gaertnera razakamalalana* is also similar to *G. macrostipula*, which is found widely in Madagascar and known from similar habitats; *G. macrostipula* can be recognized by its larger calyx, 2–3.5 mm wide, with well-developed lobes, 1–3.5 mm long, and larger corollas with tubes 6.5–9 mm long. *Gaertnera razakamalalana* is also similar to *G. macrobotrys*, another widely distributed species; *G. macrobotrys* can be recognized by its larger corollas with tubes 6.5–10 mm long and 1.5–3.5 mm in diameter and distribution at higher elevations, 400–1100 m. *Gaertnera razakamalalana* is also similar to *G. breviflora*, which is found in similar habitats in southeastern Madagascar; *G. breviflora* can be recognized by its leaves that are apically acute to obtuse or rounded and usually also shortly acuminate, with the tips 3–10 mm long, stipule tubes that are not inflated, and larger bracteoles 1–4.5 mm long.

Paratypes. MADAGASCAR. **Toamasina:** Analanjirofo, Île Sante Marie, Lokintsy, Sahasifotra, forêt littorale d'Ambohidena, 16°51′S, 49°57′E, *S. N. Andrianarivelo, D. Rabehevitra, R. Razakamalala & Poity 84* (MO), *G. McPherson, J. Rabenantoandro & R. Razakamalala 18886* (MO), *R. Rabevohitra, R. Razakamalala & Poity 5011* (MO); 10 km N Fenerive-Est, Station Forestière Tampolo, 17°17′S, 49°25′E, *P. De Block, J. Tosh & F. Rakotonasolo 1816* (BR, MO), *R. E. Gereau, P.-J. Rakotomalaza, C. Rasolomanana, T. Razafindrabeaza, S. Rapanarivo & F. Andriatsiferana 5712* (K, MO), *L. C. Raholivelo, B. Takotoninina & B. Rakotoandahy 77* (MO); Soanierana-Ivongo, Manompana, Pointe Larree, Tanambao Ambodimanga, forêt d'Andakibe, *L. Nikolov 1783* (MO), forêt d'Antanambao-Ambodimanga, 16°46′S, 49°42′–43′E, *R. Rabevohitra, J. Rabenantoandro & R. Razakamalala 4330* (MO), *R. Razakamalala, G. McPherson & J. Rabenantoandro 495* (K, MO).

36. Gaertnera robusta C. M. Taylor, sp. nov. TYPE: Madagascar. Fianarantsoa: Vatovavy-Fitovinany, Andranobetokana, Ampasimadinika, Marofototra-Mananjary, 20°50′S, 48°05′E, 450 m, 15–22 Jan. 1999, *F. Ratovoson & F. Randiantafika 13* (holotype, MO-5682745!; isotypes, P n. v., TAN n. v.). Figure 2A–C.

Haec species a *Gaertnera macrostipula* Baker stipularum costis bene evolutis, lobis calycinis brevioribus, corolla alba graciliore, pedunculo plerumque longiore atque inflorescentiae parte ramosa pyramidali ad anguste pyramidali distinguitur.

Shrubs and small trees to 11 m tall, drying brown or greenish brown; branchlets 6–9 mm diam., quadrangular, glabrous. Leaves opposite; blades obovate, 10–28 × 6–15 cm, drying chartaceous to subcoriaceous and matte, glabrous on both surfaces, at base acute to cuneate or occasionally obtuse, at apex rounded to truncate or obtuse and occasionally acuminate with deltate tips 3–6 mm; secondary veins 6 to 9 pairs, abaxially prominulous, without domatia or with few to several pilosulous domatia deeply embedded in vein axils, with intersecondary and tertiary venation not or weakly visible abaxially; petioles 8–30 mm glabrous; stipules tubular, glabrous, drying papery to chartaceous and brown, generally persistent, tube (6)10–20 mm, smooth in upper portion, with flattened wings 0.5–1 mm wide encircling petioles and extending onto stipule tube, then angled to middle of each interpetiolar side and extending 1/4–1/2 of length of tube, at apex with 2 or 4 slits, with 4 narrowly triangular lobes 1–2 mm. Inflorescences laxly cymose, many-flowered (50+), terminal on principal branches, erect, moderately to densely puberulous-pilosulous often in lines or patches, pedunculate; peduncle 6–15 cm; branched portion 8–18 × 6–26 cm, pyramidal to narrowly pyramidal, branched to 3 to 5 orders; bracts narrowly triangular, 3–22 mm, or sometimes foliaceous; bracteoles ovate, lanceolate, or ligulate, 2–5 mm; pedicels 1–3 mm. Flowers mixed sessile and pedicellate, distylous, 5-merous; calyx cupuliform, 2.5–3.5 mm wide, externally puberulous to glabrous, internally glabrous, tube 1.8–2.5 mm, regularly to irregularly lobed, lobes 5, triangular, 0.8–1.1 mm, subequal; corolla obtuse to rounded or subtruncate in bud, at anthesis salverform, white, externally glabrescent on tube and sparsely to densely puberulous on lobes, internally densely barbate in upper part of tube and onto lobes, tube 6–8 mm, cylindrical to funnelform, 1–1.2 mm diam. near middle, lobes narrowly triangular, 2.5–3 mm, at apex smooth

abaxially, adaxially shortly hooked; anthers in long-styled form ca. 1.2 mm, partially exserted, in short-styled form not seen; stigmas in long-styled form 0.8–1 mm long, exserted, in short-styled form 1–1.2 mm, included, positioned in upper part of corolla tube. Drupes subglobose to ellipsoid, 5–6 × 6–8 mm, white becoming blue, blue-violet, blue-black, or black, sometimes with persistent calyx lobes apparently elongating, to 2 mm; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera robusta* is known from humid forests on sandy soils and brown soils at 5–450(–600) m in eastern Madagascar, in the provinces of Toamasina (Analanjirofo and Atsinanana) and Fianarantsoa (Atsimo-Atsinanana and Vatovavy-Fitovinany). *Gaertnera robusta* has been collected in flower in January, February, November, and December and in fruit in January, February, April, May, and November.

IUCN Red List category. *Gaertnera robusta* is present in the protected areas of Betampona and Zahamena and the conservation sites of Analalava and Mahabo, but subpopulations outside of protected areas are expected to experience continuing decline due to forest degradation and clearing. Within an EOO of 31,803 km², less than 2000 km² is actually occupied (AOO) and only 10 locations are known; thus, *G. robusta* is here considered to be Vulnerable [VU B2ab(iii)].

Discussion. *Gaertnera robusta* can be recognized by its combination of well-developed, generally persistent tubular stipules, thick-textured, medium-sized to rather large leaves with the apices generally broad to rounded and the tertiary venation mostly not visible, relatively large inflorescences with well-developed peduncles, shortly lobed calyx limbs, and slender white corollas. The species epithet refers to the rather large leaves and inflorescences. Several specimens report that the indigenous name is "sadodoka" (*Reserves Naturelles 2324*, *Service Agricoles 1077*) or "dodoka" (*Service Forestier 15327*).

Gaertnera robusta can be confused with *G. macrostipula*, which is widely distributed in Madagascar and found in similar habitats; *G. macrostipula* can be recognized by its generally funnelform and rather inflated stipules, inflorescences with the branched portion corymbiform-rounded and the peduncles shorter, 2.5–7 cm long, calyx limb with the lobes 1–3.5 mm long and generally with some lobes more than 1.5 mm long, and pink corollas with stouter tubes, 1.3–3.5 mm in diameter (for contrasting characters of *G. robusta*, see its description above). These two species apparently also differ somewhat in phenology, with *G. macrostipula* collected in flower in January through March and in August and *G. robusta* in November through Februrary. *Gaertnera robusta* is also similar to *G. breviflora*, which is found in southeastern Madagascar in similar habitats; *G. breviflora* can be recognized by its shorter corollas with tubes 2–3 mm long and smaller truncate to denticulate calyx limbs, with the tube 1–1.2 mm long and the teeth up to 0.3 mm long or occasionally with a single lobe 0.8–1.1 mm long. *Gaertnera robusta* is also similar to *G. arenaria*, which is widely distributed in Madagascar and found in similar habitats; *G. arenaria* can be recognized by its stipules with four well-developed longitudinal ribs and four lobes 2.5–5 mm long, calyx that is truncate or denticulate with the lobes up to 0.5 mm long, and larger corollas with tubes 10–16 mm long and 1.8–4.5 mm in diameter.

Paratypes. MADAGASCAR. s. loc., *Reserves Naturelles 64-RN* (K, MO, P); Prov. Betsimisaneka du Centre, *Anonymous 303* (MO, P). **Fianarantsoa:** Atsimo-Atsinanana, environs de Vondrozo, *J. Bosser 18700* (MO, P); Farafangana, Mahabo-Mananivo, Mahabo, 23°08′S, 47°43′E, *J. Rabenantoandro, G. McPherson & Ratiana 638* (K, MO). Vatovavy-Fitovinany, Belambo forest, 22°04′S, 47°56′E, *J. Tosh, P. De Block & F. Rakotonasolo 358* (BR, K, MO). **Toamasina:** Analanjirofo, Toamasine II, Anterina, Mitanoka, Reserve Naturelle Intégrale 3 Zahamena, 17°44′–46′S, 48°54′–49°01′E, *N. M. Andrianjafy, L. Randrianjanaka, S. Rakotonandrasana & B. Tandriamampvonjy 240* (MO), *L. M. Randrianjanaka & B. M. J. Arnaud 28* (K, MO); along Rte. 5 from Fenerive to Maroantsetra, *T. B. Croat 32549* (MO); ca. 5 km S of Fenerive along Rte. 5, *T. B. Croat 32604* (MO); Fenerive Est, Station Forestiêre Tampolo, 17°16′S, 49°25′E, *R. E. Gereau, P.-J. Rakotomalaza, C. Rasolomalana, T. Razafindrabeaza, S. Rapanarivo & F. Andriatsiferana 5730* (K, MO), *Service Agricoles 1077* (MO, P), *Service Forestier (P. Zarah) 15327* (K, MO, P), *Service Forestier 17917* (K, MO, P), *J. L. Zarucchi, E. Rakotobe, A. Randrianasolo & A. Pool 7393* (K, MO). Atsinanana: Distr. Tamatave, Rendrirendry, Reserve Naturelle Intégrale de Betampona, 17°55′S, 49°13′E, *M. Andrianarisata 102* (MO), *Reserves Naturelles (Rakotoniania) 2324* (MO, P); Foulpointe, Analalava Forest Reserve, 17°43′S, 49°27′E, *M. Briggs 196* (K, MO), *J. Tosh, P. De Block & R. Rakotonasolo 86* (BR, MO).

37. Gaertnera rubra C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Analanjirofo, Zahamena RNI, O de la rivière Iofika, NO de village Bongabe, Miarinarivo, Vavatenina, 17°43′S, 48°59′E, 600 m, 20 Oct. 1994, *L. M. Randrianjanaka 214* (holotype, MO-04975860!; isotypes, K n. v., P n. v., TAN n. v.). Figure 6C–E.

Haec species a *Gaertnera obovata* var. *sphaerocarpa* (Baker) Malcomber foliis plerumque majoribus, calyce

longiore atque corolla violacea usque rubra rosea aurantiaca violacea vel alba tubo longiore distinguitur.

Shrubs or small trees to 5 m tall, drying dark brown; branchlets 5–10 mm diam., quadrangular to subterete, glabrous. Leaves opposite; blades oblanceolate to obovate, 14–33 × 4.5–11.5 cm, drying papery to chartaceous and matte, glabrous on both surfaces, at base acute to cuneate, at apex acuminate with deltate tips 5–10 mm; secondary veins 8 to 16 pairs, prominulous to prominent abaxially, without domatia or occasionally with irregular patches of pilosulous or hirsute pubescence along midrib and/or basal part of secondary veins, with intersecondary and some tertiary veins visible abaxially; petioles 10–40 mm, glabrous; stipules calyptrate, glabrous, drying membranaceous and dark brown, caducous or often fragmentating, 25–35 mm (or perhaps longer), apparently smooth, with flattened wings 1–2 mm wide encircling petioles, apex with 1 incision, complete apex not seen. Inflorescences cymose, many-flowered (40+), terminal on principal branches, erect, glabrous, sessile to pedunculate, peduncle to 10.5 cm; branched portion pyramidal, 3.5–10 × 5–14 cm, branched to 3 to 4 orders; bracts deltate, ligulate, ovate, or 3-lobed, 1–3 mm, sometimes becoming scarious, or bracts subtending basalmost secondary axes sometimes foliaceous; bracteoles triangular to ligulate, 1–2 mm; pedicels to 2 mm. Flowers mixed sessile, subsessile, and pedicellate, distylous, 5-merous; calyx cupuliform to funnelform, 3–3.5 mm wide, internally and externally glabrous, tube 2.5–3 mm, denticulate, teeth 5, triangular, to 0.5 mm; corolla in bud obtuse, at anthesis salverform, violet, red, pink, orange, or white, externally glabrous, internally densely villosulous in upper half of tube, tube 9–11 mm, cylindrical, ca. 1.2 mm diam. near middle, lobes narrowly triangular, ca. 4 mm, at apex smooth abaxially, adaxially with thickened hook; anthers in long-styled form ca. 3 mm, included, positioned in upper part of corolla tube, in short-styled form ca. 2.5 mm, shortly exserted; stigmas in long-styled form ca. 1 mm, exserted, in short-styled form ca. 1.5 mm, included, positioned in basal part of corolla tube. Immature drupes ovoid to subglobose, 8–9 mm; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera rubra* is known from humid to subhumid forests at 500–1040 m in eastern Madagascar in the province of Toamasina (Alaotra-Mangoro, Analanjirofo, and Atsinanana). *Gaertnera rubra* has been collected in flower in September and October and in fruit in January and December.

IUCN Red List category. *Gaertnera rubra* is present in the protected areas of Makira and Zahamena and the conservation site Vohibe, but subpopulations outside of protected areas are expected to experience continuing decline due to forest degradation and clearing. With a restricted geographic range size (EOO = 5937 km²; AOO ca. 4600 km²) and only seven locations, *G. rubra* is here considered Vulnerable [VU B1ab(iii)].

Discussion. *Gaertnera rubra* can be recognized by its combination of relatively large obovate or elliptic-obovate leaves, spathaceous stipules, inflorescences with relatively stout axes that are generally overtopped by the leaves, and white to usually pink, red, violet, or orange corollas with well-developed tubes. The species epithet refers to the red corolla color that is frequent in this species but unusual in *Gaertnera*.

Gaertnera rubra is similar to *G. obovata* var. *sphaerocarpa*, which is widely distributed in Madagascar; *G. obovata* var. *sphaerocarpa* can be separated by its generally smaller leaves, 6–23.5 × 1.8–9 cm, with generally fewer secondary veins, 5 to 11 pairs; shorter calyx, with the tube 1.5–2 mm long; and white to pink corollas with shorter tubes, 4–8 mm long (for contrasting characters of *G. rubra*, see its description above).

Paratypes. MADAGASCAR. **Toamasina:** Alaotra-Mangoro, Antsianaka, *Humblot 422* [additional penciled number under this, "*424*"] (K, MO, P); Analanjirofo, Vavatenina, Parc Nat. Zahamena, Rivière Sahemora, 17°38′S, 48°53′E, *N. M. Andrianjafy, R. Ratovoson, S. Takotondrasana, L. Randianjanaka, P. Manenjaka & Gonata 179* (K, MO); Maroantsetra, Rantage, Morafeno, village of Behovana, 15°48′S, 49°32′E, *P. Antilahimena & Landrice 2253* (MO); Maroantsetra, Ambinanitelo, Marovovovonana, near village of Ambatofotsy, Mangabe forest, 15°18′S, 49°29′E, *P. Antilahimena 2659* (MO); Maroantsetra, Antsirabesahatany, Anjiahely, 15°24′S, 49°26′E, *P. Antilahimena, Pascal & Ramarosahana 1486* (MO); W of Vavatenina, Réserve Naturelle Intégrale Zahamena, forest of Amboditamenaka, 17°44′S, 49°00′E, *S. T. Malcomber, B. Rasolondraibe, L. Randrianjanaka & J. Abraham 2553* (MO); en dehors du PN de Zahamena, *R. Rakotondrajaona 151* (MO); Atsinanana, Ambinanindrano II, Ambalabe, Vatomandry, NO du Toin'i Foara, 19°10′S, 48°35′E, *R. Ranaivojaona, A. Randrianasolo, A. Razanatsima, Pierrot, Dada & Naivo 977* (MO).

38. Gaertnera schatzii Malcomber, Ann. Missouri Bot. Gard. 96(4): 651, fig. 2. 2009. TYPE: Madagascar. Toamasina: Analanjirofo, Masoala Nat. Park, Antalvia, 15°47′S, 50°02′E, 13–16 Nov. 1989, *G. E. Schatz, J. Dranfield, S. Dransfield, D. DuPuy & B. DuPuy 2808* (holotype, MO; isotypes, K, P, TAN, WAG).

Distribution and IUCN Red List category. *Gaertnera schatzii* is found in northeastern Madagascar in

the province of Toamasina at 0–380 m. It is known only from a single location wholly encompassed within the Masoala protected area at Antalavia. In the absence of population size information and with no decline projected within the conservation area, *G. schatzii* is here considered to be of Least Concern (LC). Although no decline is expected within the protected area at Antalavia, low (< 1000 mature individuals) population size information might reveal an intrinsic risk of extinction and therefore threatened status.

See Malcomber and Taylor (2009: 651–652) for species description.

39. Gaertnera sclerophylla C. M. Taylor, sp. nov. TYPE: Madagascar. Fianarantsoa: Atsimo-Atsinanana, S of Farafangana, near village of Mahabo, littoral forest on sand, 23°11′S, 47°42′E, 25 m, 11 Nov. 2001, *G. McPherson & J. Rabenantoandro 18404* (holotype, MO-5888592!; isotypes, K n. v., TEF n. v.). Figure 7C–E.

Haec species a *Gaertnera obovata* Baker var. *sphaerocarpa* (Baker) Malcomber foliis basi obtusis usque rotundatis domatiis nullis perpaucisve, venatione tertiaria non manifesta atque stipularum parte tubulari plerumque persistente distinguitur; etiam sylvas littorales ad altitudines 10–120 m habitat.

Shrubs and small trees to 12 m tall, drying greenish brown; branchlets 3–5 mm diam., quadrangular, glabrous. Leaves opposite; blades obovate or oblanceolate, 6.5–26 × 3–11 cm, drying chartaceous to subcoriaceous and matte to somewhat shiny, glabrous on both surfaces, at base rather abruptly obtuse to rounded, at apex obtuse, rounded, or truncate then sometimes with broad acuminate tips 1–3 mm; secondary veins 5 to 7 pairs, plane to thinly prominulous abaxially, without domatia or some leaves with a few weakly developed foveolate domatia, with secondary venation generally visible, intersecondary and tertiary venation not visible or weakly developed abaxially; petioles 6–30 mm, glabrous; stipules calyptrate, glabrous, drying papery and dark brown or reddish brown, usually fragmenting with tubular basal portion persisting on 1 to 5 apical nodes or occasionally fully deciduous, 15–25 mm, smooth, wings absent or sometimes tardily developing, rounded, ca. 0.5 mm wide, encircling only underside of petiole, apex with 1 or 2 incisions, with 2 triangular lobes 1–2 mm, puberulous to glabrous. Inflorescence laxly cymose, many-flowered (50+), terminal on principal branches, erect, moderately to densely puberulous to pilosulous, peduncule; peduncle 3–8 cm; branched portion pyramidal, 6–14 × 5.5–15 cm, branched to 3 to 4 orders; bracts deltate to linear, 1–2 mm; bracteoles ligulate to triangular, 0.5–1 mm. Flowers sessile or subsessile, distylous, 5-merous; calyx cupuliform, 1.5–2 mm wide, glabrous externally, internally glabrous except with a strigillose to puberulous ring near base, tube 1–1.5 mm, subtruncate to denticulate, teeth 5, triangular, to 0.4 mm; corolla in bud obtuse to truncate, at anthesis salverform, white, externally glabrous, internally densely barbate in upper part of tube, tube 4–6 mm, cylindrical ca. 1 mm diam. near middle, lobes narrowly triangular, ca. 2 mm, at apex abaxially smooth, adaxially shortly thickened to hooked; anthers in short-styled form 1.5–1.8 mm, exserted, in long-styled form ca. 2 mm, partially exserted; stigmas in short-styled form ca. 1.8 mm, included, positioned in upper part of corolla tube, in long-styled form ca. 0.8 mm, exserted. Drupes subglobose, 7–10 mm diam., blue, blue-black, or perhaps white; pyrenes 2, hemispherical, smooth abaxially.

Habitat, distribution, and phenology. *Gaertnera sclerophylla* is known from littoral forest on sandy substrates and from humid forests on laterite at 10–30(–120) m in eastern and southeastern Madagascar, in the provinces of Toamasina (Atsinanana), Fianarantsoa (Atsimo-Atsinanana and Vitovavy-Fitovinany), and Toliara (Anosy). *Gaertnera sclerophylla* has been collected in flower in August and October through December, and in fruit January through April.

IUCN Red List category. *Gaertnera sclerophylla* is known from Fort Dauphin to Ambila-Lemaitso. Although it is present in the protected area of Manombo and the conservation sites of Mahabo, Petriky, and Sainte Luce, its subpopulations outside of conservation areas are expected to experience continuing decline due to forest degradation and clearing. With a restricted geographic range size (EOO = 8145 km²; AOO < 500 km²) and only seven locations, *G. sclerophylla* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera sclerophylla* can be recognized by the combination of its firm-textured, calyptrate stipules that generally persist as a tube around the stem; stiff-textured leaves that are oblanceolate to obovate, not shiny, abruptly obtuse to rounded at the base, generally without domatia, and generally with the tertiary venation not visible; lax cymose inflorescences; rather small, generally white corollas; subtruncate to denticulate calyx limbs; and habitat in littoral forest, with most of the collection from 10 to 30 m elevation, and one (*Davis et al. 2150*) from higher, at 120 m. The species

epithet refers to the tough-textured leaves. The stipules characteristically split for about a third of their length along one or two incisions, forming, respectively, one asymmetric apical portion or two broadly triangular apical portions. In some cases the stipules appear to be tubular, and this species is keyed as having both calyptrate and tubular stipules to facilitate its identification. Specimen notes report variously blue to blue-black or white as the mature color of the fruits; this variation is uncommon in species of Rubiaceae but not unknown; for more information see the discussion of *G. obovata* var. *sphaerocarpa*.

Gaertnera sclerophylla is similar to *G. obovata* var. *sphaerocarpa*, which is widely distributed in Madagascar; *G. obovata* var. *sphaerocarpa* can be recognized by its usually thin-textured caducous stipules and generally thinner-textured, chartaceous leaves that are acute to cuneate at the base and have regularly developed domatia and the tertiary venation generally regularly visible (for contrasting characters of *G. sclerophylla*, see its description above). These two species are not completely separable by flower characters, but in addition to the differences in their leaves and stipules they are found in different habitats with *G. obovata* var. *sphaerocarpa* known from humid forests at 360 m and above.

Several morphologically similar species of *Gaertnera* with calyptrate stipules are known from littoral forests. Among these, *G. xerophila* (described later in this article) is found in east-central Madagascar and can be recognized by its thick-textured, subcoriaceous to coriaceous leaves with the venation generally not visible, calyx limb with lobes up to 1.2 mm long, and smaller corollas with tubes ca. 2.5 mm long. *Gaertnera guillotii* is found along nearly the entire east coast of Madagascar, and can be recognized by its somewhat smaller leaves, 1.7–13.2 × 0.7–4.6 cm, with regularly developed domatia and the tertiary venation generally not visible, generally smaller inflorescences with the branched portion 0.6–7 × 0.8–6.2 cm, and caducous stipules with four longitudinal ridges on the tubular portions. Some other similar species are also found in littoral forests but differ from the previously mentioned species in having tubular stipules. Among these, *G. nitida* is found in northwestern Madagascar, and can be recognized by its generally shiny leaves with the tertiary venation finely reticulated and visible although plane and generally regularly developed domatia. *Gaertnera macrostipula* is widely distributed in Madagascar and can be recognized by its well-developed persistent stipules with the tube often inflated, generally covering most or all of the internode above it, and becoming marcescent along the margins; generally larger flowers with corolla tubes 6.5–9 mm long; and calyx limbs with short to well-developed lobes 0.5–3.5 mm long. *Gaertnera breviflora* is found in southeastern Madagascar and can be recognized by its relatively small corollas, with the tube 2.5–3 mm long.

Paratypes. MADAGASCAR. **Fianarantsoa:** Atsimo-Atsinanana, Farafangana, Rés. Spec. Manombo, 23°01′–02′S, 47°43′–44′E, *A. P. Davis, F. Rakotonasolo & P. De Block 2150* (K, MO), *J. Rabenantoandro, G. McPherson & Gervais 772* (MO); Farafangana, Mahabo, 23°11′S, 47°42′E, *R. Ludovic & J. Emilson 968* (MO, TAN), *R. Razakamalala & D. Rabehevitra 704* (K, MO). **Toamasina:** Atsinanana, Ambila-Lemaitso, 18°53′S, 49°08′E, *Boiteau 490* (MO), *A. J. M. Leeuwenberg 13794* (K, MO), *S. T. Malcomber, A. Davis, D. Gower & J. Andriantiana 2914* (MO), *2916* (MO); Mahanoro, Ambodibonara, Ambalavontaka, forêt d'Antalamalotra (Antaimby Kely), 20°23′S, 48°33′E, *R. Ranaivojaona, R. Razakamalala & G. Paul 850* (K, MO); 4 km S Vatomandry, 19°24′S, 048°57′E, *J. Tosh, P. De Block & F. Rakotonasolo 66* (K, MO); Vatovavy-Fitovinany, Mahanoro, Ambodibonara, Ambalavontaka, forêt d'Antaimby, 20°22′S, 48°34′E, *R. Ranaivojaona, R. Razakamalala, Z. Rogers & P. Seth 637* (MO). **Toliara:** Anosy, St. Luce, along Rte. Nationale 13, 24°46′S, 47°09′E, *P. De Block, F. Rakotonasolo, Randriamboavonjy, S. Dessein & Leyman 649* (MO); Sainte Luce, Fort-Dauphin, forêts littorales, 24°46′S, 47°10′E, *L. Faliniaina, J. Rabenantoandro & E. Ramisy 35* (MO); N Fort Dauphin (Tôlañaro), near Ste. Luce (Manofiafy), 24°47′S, 47°10′E, *G. McPherson, N. Dumetz & R. Rabevohitra 14223* (K, MO).

40. Gaertnera velutina C. M. Taylor, sp. nov. TYPE: Madagascar. Fianarantsoa: Haute Matsiatra, Ranomafana Nat. Park, Vohiparara, 21°14′S, 47°24′E, 1100–1200 m, 2 Nov. 1997, *S. T. Malcomber, A. P. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2863* (holotype, MO-5899033!; isotypes, P n. v., TAN n. v.). Figure 8D–G.

Haec species a *Gaertnera phanerophlebia* Baker stipulis tubularibus lobis calycinis atque corollis omnibus brevioribus distinguitur.

Shrubs and small trees to 8 m tall, drying brown or reddish brown; branchlets 3–5 mm diam., flattened, densely hirtellous to tomentulose with trichomes drying reddish brown, sometimes becoming glabrescent. Leaves opposite; blades oblanceolate to elliptic-oblanceolate or elliptic-oblong, 6.5–14 × 2.5–6.5 cm, drying chartaceous to subcoriaceous and matte, adaxially glabrous, abaxially densely hirtellous to tomentulose on midrib to throughout, at base acute to cuneate, obtuse, or infrequently rounded, at apex obtuse to acuminate with tips 2–8 mm; secondary veins 7 to 10 pairs, abaxially prominent, without domatia, with higher-order venation hardly or not visible abaxially; petioles 4–15 mm, hirtellous to

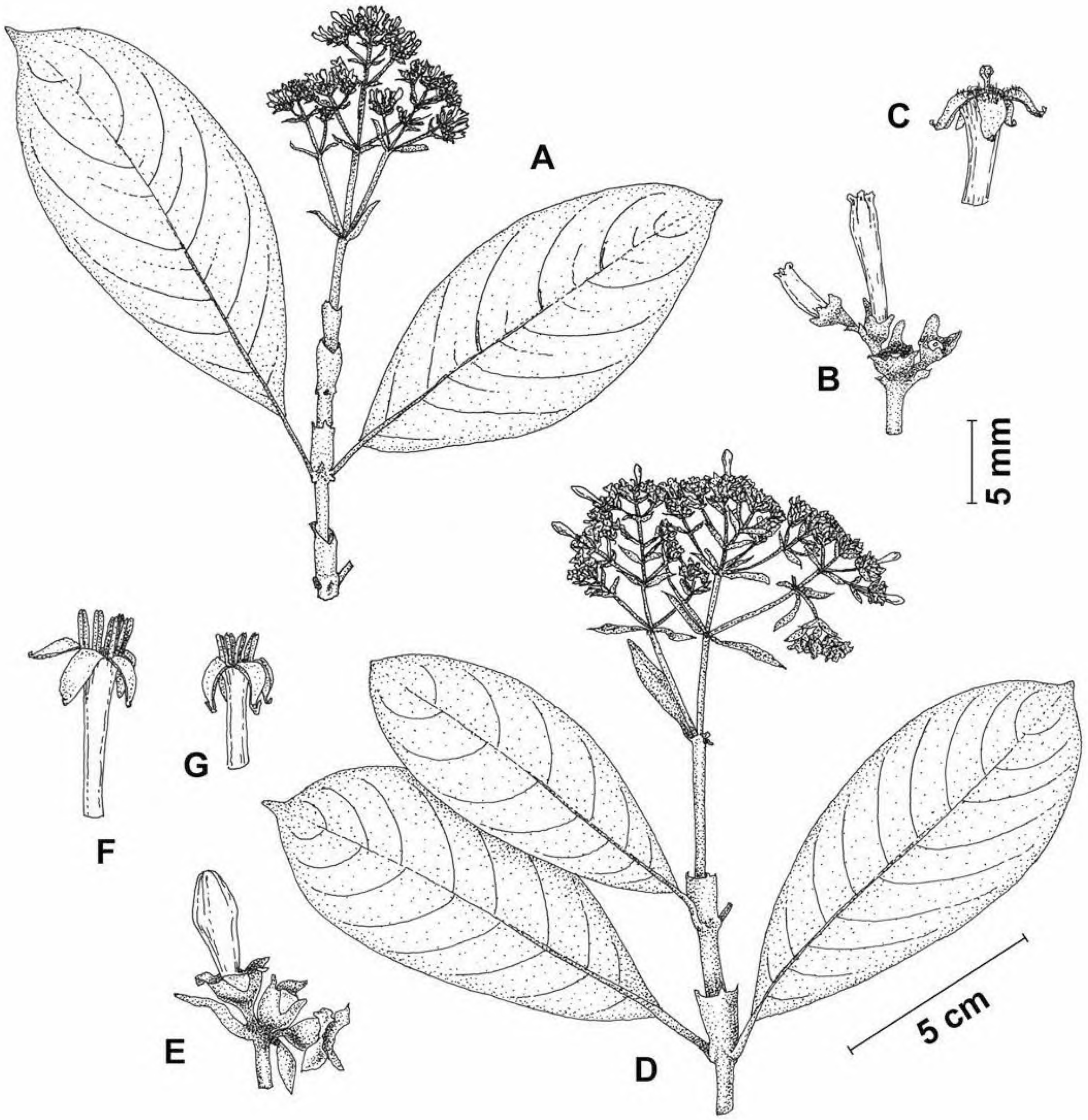


Figure 8. A–C. *Gaertnera vernicosa* C. M. Taylor; based on *R. Ranaivojoana et al. 959* (MO). —A. Flowering branch. —B. Portion of inflorescence with two flower buds and two flowers from which corollas have fallen. —C. Corolla at anthesis, with style, dissected off flower. D–G. *Gaertnera velutina* C. M. Taylor. —D. Flowering branch. —E. Portion of inflorescence, with one flower bud and two flowers from which corollas have fallen. —F. Corolla, dissected off flower, with relatively longer tube; based on *P. De Block 1751* (MO). —G. Corolla, dissected off flower, with relatively shorter tube. D, E, G based on *B. Lewis et al. 880* (MO). A, D, to same 5-cm scale; B, C, E–G, to same 5-mm scale.

tomentulose; stipules tubular, densely strigillose to tomentulose, drying papery and brown, persistent on 2 to 5 apical nodes or sometimes tubular portion dehiscing at base but remaining around stem, tube 6–16 mm, with wings ca. 1 mm wide encircling petioles and uniting just above base of tube, at apex generally not split, subtruncate to acute, with lobes 4, narrowly triangular to linear, 1–4 mm. Inflorescences rather laxly cymose, many-flowered (40+), terminal on principal branches, erect, densely hirtellous to strigillose, pedunculate; peduncles 2–6 cm; branched portion corymbiform, 4–10 × 5.5–11 cm, branched to 3 or 4 orders; bracts narrowly elliptic to narrowly triangular, 3–25 mm; bracteoles triangular to lanceolate, 1–7 mm, inserted below or often at base of calyx and sometimes fused to it; pedicels to 1 mm. Flowers mixed subsessile and pedicellate, distylous, 5-merous; calyx cupuliform, 2.5–3.5 mm wide, externally densely strigillose or tomentulose-strigillose, internally densely strigillose in upper part and glabrous in lower part, tube 2–3 mm, lobed, lobes 5, triangular, 1.5–3 mm, equal to somewhat unequal; corolla in bud obtuse, at anthesis salverform, white or sometimes pink, externally sparsely to densely

strigillose-puberulous, internally glabrous except with pilosulous ring in upper part of tube, tube 5.5–8(10) mm, cylindrical, 1.2–1.5 mm diam. near middle, lobes narrowly triangular, 2–3 mm, at apex abaxially smooth, adaxially shortly hooked; anthers in short-styled form ca. 2 mm, included, positioned in upper part of corolla tube, in long-styled form ca. 2 mm, partially exserted; stigmas in short-styled form ca. 2 mm, included, positioned near middle of corolla tube, in long-styled form ca. 2 mm, linear, positioned in mouth of corolla tube. Immature drupes ovoid, ca. 5 mm diam.; pyrenes 2, hemispherical, abaxially smooth.

Habitat, distribution, and phenology. *Gaertnera velutina* is known from subhumid forests at (250–) 750–1400 m in eastern Madagascar, in the provinces of Finarantsoa (Haute Matsiatra, Ihorombe, and Vatovavy-Fitovinany), and Toamasina (Atsinanana). *Gaertnera velutina* has been collected in flower in August through December and in young fruit in January.

IUCN Red List category. *Gaertnera velutina* is found in the protected areas of Andringitra and Ranomafana. With a restricted geographic range size (EOO = 3625 km^2; AOO ca. 1850 km^2), an expected decline of subpopulations outside of protected areas due to habitat degradation and conversion, and only eight known locations, *G. velutina* is here considered to be Vulnerable [VU B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera velutina* is characteristically evenly and shortly pubescent on the stems, stipules, and leaf undersurfaces, giving the plants a velvety appearance; the species epithet refers to this appearance. This new species is generally similar in overall aspect and pubescence to *G. phanerophlebia*, which is found in northern and northeastern Madagascar, in particular the leaves with the higher-order venation mostly not visible are similar in both species; however, *G. phanerophlebia* can be separated by its calyptrate stipules, densely congested to subcapitate inflorescences, usually longer calyx lobes 2–14 mm long, and larger corollas with tubes 9.5–17 mm long (for contrasting characters of *G. velutina*, see its description above). *Gaertnera velutina* is also similar to *G. macrostipula*, which is widely distributed in Madagascar; *G. macrostipula* can be recognized by its generally larger stipules, 12–35 mm long, that are mostly long enough to largely or completely cover the stem up to the next higher node and are irregular along the margins. *Gaertnera velutina* is also similar to *G. hispida*, *G. hirsuta*, and *G. obovata* var. *sphaerocarpa*, one or more of which can be found in most humid vegetation regions of Madagascar; these can all be recognized by their calyptrate stipules.

The specimen *De Block et al. 1751* was collected in a different part of the country from the other specimens included here, at a lower elevation, and in flower a little later in the season, and it may also differ from the others in its slightly longer corolla tubes, ca. 10 mm long (Fig. 8F). Otherwise this specimen cannot be separated morphologically from the remaining specimens included here in *G. velutina*. Few mature corollas have been collected in total, so the range of variation in corolla size in *G. velutina* from higher elevations may be incompletely known.

Paratypes. MADAGASCAR. **Fianarantsoa:** Haute-Matsiatra, Ranomafana Natl. Park, Vohiparara, 21°14′S, 47°24′E, *S. T. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2861* (K, MO), 21°14′S, 47°22′E, *S. T. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2871* (MO), *S. T. Malcomber, A. Davis, D. Gower, J. Andriantiana & A. Kotozafy 2872* (MO); Ifanadiana, Ranomafana, Ranomena, Ampandriambazaha, 21°13′S, 47°26′E, *F. Rakotonasolo RNF 848* (BR, K, MO, TAN); Ihorombe, haute vallée de la Rienana (bassin du Matitanana), 22°15′S, 47°09′E, *H. Humbert 3450* (MO, P); ca. 43 km S of Ambalavao, Andringitra Reserve, jct. of Sahanivoraky & Sahavatoy rivers, 22°14′S, 47°00′E, *B. Lewis, J. Raharimalala, G. Rahajasoa, M. Randiambololona & J. McDonagh 880* (K, MO), ca. 40 km S of Ambalavo, Andringitra Reserve, along tributary of Sahavatoy River, 22°13′S, 46°58′E, *B. Lewis, J. Raharilala, P. J. Rakotomalala, M. Andrianarisata & J. McDonagh 958* (MO); Rés. Nat. Int. no. 5 Andringitra, Ivongo, Ambahatsy, 22°14′S, 47°00′E, *C. Rakotovao, M. Zjhra, J. Hutcheon & J.-B. Razafindrabe 83* (K, MO), *J. B. Razafindrabe, C. Rakotovao, M. Zhjra & J. Hutcheon 120* (MO); Andringitra, au NO d'Ambarongy, *C. Rakotovao 224* (MO); Vatovavy-Fitovinany, entre Fianarantsoa & Ranomafana, 38 km après Fianarantsoa, 21°16′S, 47°21′E, *P. De Block, S. Dessein, F. Rakotonasolo & Randiamboavonjy 621* (BR, MO); Massif d'Andrambovato, Tolongoina, Ikongo, 21°31′S, 47°26′E, *S. G. Razafimandimbison 342* (MO); Fanadiana, Parc Nat. Ranomafana (Miaranony), 21°08′S, 47°37′S, *R. Razakamalala, L. Andriamahefarivo & A. Kotozafy 239* (MO); Ranomafana, 19°06′S, 48°42′E, *H. van der Werff, S. T. Malcomber, B. Gray & S. Rapanarivo 12663* (K, MO). **Toamasina:** Atsinanana, PK 83 on rd. Moramanga–Brickaville, 18°58′S, 48°47′E, *De Block, J. Tosh & F. Rakotonasolo 1751* (BR, MO).

41. Gaertnera vernicosa C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Atsinanana, Vatomandry, Ambalabe, W of Vakoanina Toby, trail to Sahamahirana River, 19°10′S, 48°35′E, 638 m, 21 Nov. 2004, *A. Randrianasolo, R. Ranaivojaona & A. Razanatsima 893* (holotype, MO-5901079!; isotypes, P n. v., TAN n. v.). Figure 8A–C.

Haec species a *Gaertnera nitida* C. M. Taylor stipularum alis petiolum circumcinctis, lobis calycinis insigniter inaequalibus atque corolla longiore lobis abaxialiter incrassatis distinguitur.

Shrubs and small trees to 7 m tall, drying dark brown; branchlets 2–5 mm diam., quadrangular, glabrous. Leaves opposite; blades elliptic, elliptic-oblong, or elliptic-obovate, 9–18 × 3–6 cm, drying chartaceous to subcoriaceous and generally shiny, glabrous on both surfaces, at base acute to obtuse or rounded, at apex obtuse to truncate and usually also with acuminate tips 2–6 mm; secondary veins 5 to 9 pairs, abaxially prominulous, usually with small foveolate domatia, with intersecondary and tertiary venation extensively reticulated, visible, and prominulous abaxially; petioles 6–15 mm, glabrous; stipules tubular, glabrous, drying chartaceous and dark brown, persistent or sometimes deciduous, tube 9–16 mm, with flattened wings 0.5–1 mm wide, encircling petioles and extending as ridges 1/4–1/2 of length of tube, apex with 1 or 2 incisions, broadly triangular, with 2 linear lobes ca. 1 mm. Inflorescences congested to somewhat laxly cymose, many-flowered (40+), erect, terminal on principal branches, moderately to densely pilosulous-puberulous, pedunculate; peduncle 0.8–5.5 cm; branched portion broadly pyramidal, 4–7 × 6–6.5 cm, branched to 3 or 4 orders; bracts ovate to narrowly triangular, 2–17 mm; bracteoles ligulate to triangular, 1–4 mm; pedicels to 2 mm. Flowers mixed sessile, subsessile and shortly pedicellate, distylous, 5-merous; calyx cup-shaped, 2–3 mm wide, externally glabrous, internally puberulous, tube 1.5–2 mm, lobed, lobes 5, triangular, 0.5–3 mm, subequal or usually unequal by up to 300%; corolla in bud truncate and knobbed at apex, at anthesis salverform, white, externally glabrous, internally barbate from upper part of tube onto lobes, tube 6–7 mm, cylindrical to weakly funnelform, 1.1–2 mm diam. at middle, lobes ligulate-triangular, 2–2.5 mm, at apex abaxially with rounded to sublingulate thickening 0.2–0.3 mm near apex, adaxially shortly hooked; anthers in long-styled form ca. 2 mm, partially exserted, in short-styled form ca. 2 mm, exserted; stigmas in long-styled form ca. 0.8 mm, exserted, in short-styled form not seen. Drupes not seen.

Habitat, distribution, and phenology. *Gaertnera vernicosa* is known from humid to subhumid forest at 536–1100 m in northeastern to east-central Madagascar, in the provinces of Antsiranana (SAVA) and Toamasina (Alaotra-Mangoro and Atsinanana). *Gaertnera vernicosa* has been collected in flower in November and has not been documented in fruit.

IUCN Red List category. *Gaertnera vernicosa* is known from only five collections from Ambalabe to south of Marojejy. Although it is present in the conservation site of Vohibe, its subpopulations outside of this conservation area are expected to experience continuing decline due to forest degradation and clearing. With a restricted geographic range size (EOO = 8427 km²; AOO ca. 7000 km²) and only four locations, *G. vernicosa* is here considered to be Vulnerable [VU B1ab(iii)].

Discussion. *Gaertnera vernicosa* can be recognized by the combination of its tubular stipules with the petiolar wings extending onto their lower portions, stiff-textured leaves that are generally shiny on both surfaces and have the extensively reticulated tertiary venation prominulous below, cymose inflorescences, calyx limbs with the lobes usually markedly unequal, and moderately sized corollas with the lobes markedly thickened abaxially near the tip, giving the flower buds a truncate and knobbed apical profile. The shiny leaves often appear varnished on dried specimens; the species epithet refers to this feature. *Gaertnera vernicosa* is similar in particular in its shiny tough leaves to *G. nitida*, which is found in northwestern Madagascar; *G. nitida* can be recognized by its leaves with the tertiary venation plane on the lower surface, calyptrate stipules, and corollas with the lobes not much thickened abaxially and consequently the flower buds acute in outline (for contrasting characters of *G. vernicosa*, see its description above).

Paratypes. MADAGASCAR. **Antsiranana:** SAVA, 8 km après Andrakata, rte. Samsana-Andapa, *P. Morat 2788* (MO). **Toamasina:** Alaotra-Mangoro, Didy à Brickaville, *G. Cours 4927* (K, MO); Atsinanana, Ambinanindrano II, Ambalabe, Vatomandry, près de Vakona, S de Tobin'i Foara, 19°10′S, 48°35′E, *R. Ranaivojaona, R. Randrianasolo, A. Razanatsima, Velomahefa, Dada & Pierrot 959* (MO); forêt de Vohibe, NO de Toby Foara, 19°10′S 48°35′E, *A. Razanatsima, F. Rakotoarivony, L. Rasoaviety, Honoré & Célestin 648* (MO, TAN).

42. Gaertnera xerophila C. M. Taylor, sp. nov. TYPE: Madagascar. Toamasina: Atsinanana, Brickaville, Firaisana, Andranonkoditra, Fokontany, Ankanin'ny nofy, forêt de Vohibola, 18°34′S, 49°15′E, 8 m, 4 Aug. 2003, *D. Rabehevitra, R. Razakamalala & J. Paul 410* (holotype, MO-5888585!; isotypes, P n. v., TAN n. v.). Figure 7F–I.

Haec species a *Gaertnera guillotii* Hochr. foliis latioribus domatiis carentibus atque limbo calycino longiore distinguitur.

Shrubs and small trees to 5 m tall, drying greenish brown to reddish brown; branchlets 3–5 mm diam.,

subquadrangular to subterete, glabrous. Leaves opposite; blades elliptic-oblong, 5.5–12 × 1.7–7.8 cm, drying subcoriaceous to coriaceous and matte, glabrous throughout, at base obtuse to rounded, at apex obtuse, rounded, or truncate and sometimes also with acuminate tips 1–3 mm; secondary veins 6 or 7 pairs, plane and not visible abaxially, without domatia, higher-order venation not visible abaxially; petioles 6–10 mm, glabrous; stipules calyptrate, glabrous, drying membranaceous and dark brown, caducous and sometimes fragmenting, 20–21 mm, smooth, with rounded wings 0.5–0.8 mm wide encircling undersides or all of petioles, at apex with 1 incision, narrowly triangular, ca. 2 mm, puberulous. Inflorescence cymose to congested cymose, many-flowered, terminal on principal branches, densely pilosulous to puberulous, sessile to pedunculate; peduncle 2–3 cm; branched portion corymbiform, 4–6.5 × 5–9 cm, branched to 3 or 4 orders; bracts narrowly elliptic to narrowly triangular, 3–8 mm, or sometimes those subtending basalmost secondary axes foliaceous; bracteoles triangular to narrowly elliptic, 1–3 mm, inserted below or often at base of or in lower portion of calyx limb. Flowers sessile to subsessile, biology unknown, 5-merous; calyx cupuliform, 2–3 mm wide, externally puberulous to glabrous, internally glabrous except puberulous to strigillose at base, tube 1.5–2.2 mm, denticulate to lobed, lobes or teeth 5, narrowly triangular to broadly triangular, 0.2–1.2 mm, a little unequal; corolla in bud obtuse to acute, at anthesis salverform, white, externally glabrous, internally densely barbate in throat, tube ca. 2.5 mm, slenderly funnelform, ca. 1 mm diam. near middle, lobes narrowly triangular, ca. 2.2 mm, at apex abaxially smooth, adaxially thickened to shortly hooked; anthers in presumed long-styled form ca. 1 mm, partially exserted; stigmas in presumed long-styled form ca. 1 mm, exserted. Immature drupes subglobose to ellipsoid and weakly flattened laterally, 4–5 × 5–6 mm; pyrenes 2, hemispherical, abaxially smooth.

Habitat, distribution, and phenology. *Gaertnera xerophila* is known from humid forest, often on sand substrates, at 0–700 m in eastern Madagascar in the province of Toamasina (Analanjirofo and Atsinanana). *Gaertnera xerophila* has been collected in flower in August and December and in fruit in February.

IUCN Red List category. *Gaertnera xerophila* is present in the protected area of Ambatovaky and the conservation site of Analalava. With a restricted geographic range size (EOO = 2318 km^2; AOO ca. 100 km^2), an expected continuing decline of the subpopulation at Vohibola, and only three locations, *G. xerophila* is here considered to be Endangered [EN B1ab(iii)+2ab(iii)].

Discussion. *Gaertnera xerophila* is known from humid vegetation but apparently at least sometimes is found in sites that are locally dry edaphically, and has very thick-textured leaves. These leaves differ from those of the other species of *Gaertnera* in their apparent adaptation for a dry environment; the species epithet refers this form. *Gaertnera xerophila* is similar in aspect and habitat to *G. guillotii*, which is found along nearly the entire east coast of Madagascar; *G. guillotii* differs in its smaller (1.7–13.2 × 0.7–4.6 cm), thinner-textured leaves with domatia, lack of or only tardy development of wings encircling the petioles, and shorter subtruncate calyx limbs 0.8–1.2 mm long (for contrasting characters of *G. xerophila*, see its description above). *Gaertnera xerophila* is also similar to *G. sclerophylla*, which is found in eastern and southeastern Madagascar; *G. sclerophylla* differs in its generally visible leaf venation, lack of or tardy development of petiole wings, shorter bracts, shorter subtruncate calyx limbs, and longer corollas with the tube 4–6 mm long and much longer than the lobes. The specimen *Rakotonoasolo et al. 682* was collected in wetter forest than the others and has somewhat smaller leaves and calyx limbs, but cannot be conclusively separated from the other specimens.

Paratypes. MADAGASCAR. **Toamasina:** Analanjirofo, Soanierana-Ivongo, Andapafito, Iampirano, Rés. Spéc. d'Ambatovaky, 4 km S of village, *F. Rakotonasolo, H. Beentje, H. Ralimanana & M. Rakotoarinivo 682* (K, MO); Atsinanana, Vohibola, forest N to NNW of village of Andranokoditra, N of Lac Ampitabe, 18°34′S, 49°15′E, *P. P. Lowry II, R. Rabevohitra, J. Rabenantoadro, R. Razakamalala & S. W. J. Lowry 6083* (K, MO, P, TAN); Brickaville, Ambinaninony, Andranokoditra, 18°33′S, 49°15′E, *J. Rabenantoandro, R. Razakamalala & J. Paul 872* (MO, P, TAN); Foulpointe, Analalava Forest Reserve, 17°43′S, 49°27′E, *J. Tosh, P. De Block & F. Rakotonasolo 89* (BR, MO, TAN).

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APPENDIX 1. Species of *Gaertnera* found in Madagascar and their conservation assessments using IUCN categories and criteria. See text for details of the conservation assessments.

G. alata Bremek. ex Malcomber & A. P. Davis, CR B2ab(iii)
G. arenaria Baker, LC
G. arenarioides C. M. Taylor, EN B1ab(iii)+2ab(iii)
G. bambusifolia Malcomber & A. P. Davis, LC
G. breviflora C. M. Taylor, VU B1ab(ii,iii,iv)+2ab(ii,iii,iv)
G. brevipedicellata Malcomber & A. P. Davis, VU B1ab(iii)-2ab(iii)
G. cardiocarpa Boivin ex Baill., EN B1ab(ii,iii,iv)+2ab(ii,iii,iv)
G. darcyana Malcomber & A. P. Davis, VU B1ab(iii)
G. drakeana Aug. DC., EN B1ab(ii,iii,iv)+2ab(ii,iii,iv)
G. furcellata (Baill. ex Vatke) Malcomber & A. P. Davis, EN B1ab(iii)+2ab(iii)
G. guillotii Hochr., LC
G. hirsuta C. M. Taylor, EN B1ab(iii)+2ab(iii)
G. hispida Aug. DC., VU B1ab(iii)+2ab(iii)
G. humblotii Drake, VU B1ab(iii)
G. ianthina Malcomber, LC
G. inflexa Boivin ex Baill., LC
G. laevis C. M. Taylor, VU B1ab(iii)+2ab(iii)
G. littoralis C. M. Taylor, EN B1ab(iii)+2ab(iii)
G. lowryi Malcomber, VU B1ab(iii)+2ab(iii)
G. macrobotrys Baker, LC
G. macrostipula Baker, LC
G. madagascariensis (Hook. f.) Malcomber & A. P. Davis, LC
G. malcomberiana C. M. Taylor, VU B1ab(iii)+2ab(iii)
G. masoalana C. M. Taylor, EN B1ab(iii)
G. microphylla Capuron ex Malcomber & A. P. Davis, EN B1ab(iii)+2ab(iii)
G. monstruosa Malcomber, VU B1ab(iii)
G. nitida C. M. Taylor, NT
G. obovata Baker, LC
G. obovata var. *obovata*, LC
G. obovata var. *sphaerocarpa* (Baker) Malcomber, LC
G. pauciflora Malcomber & A. P. Davis, NT
G. phanerophlebia Baker, LC
G. phyllosepala Baker, LC
G. phyllostachya Baker, LC
G. rakotovaoana C. M. Taylor, CR A3c
G. raphaelii Malcomber, LC
G. razakamalalana C. M. Taylor, EN B1ab(iii)+2ab(iii)
G. robusta C. M. Taylor, VU B2ab(iii)
G. rubra C. M. Taylor, VU B1ab(iii)
G. schatzii Malcomber, LC
G. sclerophylla C. M. Taylor, VU B1ab(iii)+2ab(iii)
G. velutina C. M. Taylor, VU B1ab(iii)+2ab(iii)
G. vernicosa C. M. Taylor, VU B1ab(iii)
G. xerophila C. M. Taylor, EN B1ab(iii)+2ab(iii)

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4. First Page

☐ Footnotes are typed as double-spaced paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies, herbaria that loaned specimens, and the name of the artist. The second footnote is the author's

address. Addresses for additional authors are each separate footnotes. No other footnotes occur, except in tables.

5. Abstract & Key Words

☐ A one-paragraph abstract precedes the text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
☐ The abstract is concise (1 paragraph) and includes brief statements about the paper's intent, materials and methods, results, and significance of findings.
☐ A brief list of key words immediately follows the abstract.

6. Taxonomic Treatment

☐ Species entries are organized as follows: Heading, vernacular name(s), Latin or English diagnosis (if necessary), description, distribution, summary, discussion, specimens examined. The discussions are parallel and follow the same order, e.g., diagnostic characteristics, distinction from similar species variation, distribution and ecology, nomenclature and typification, uses.
☐ One paragraph per basionym is used as follows: Taxon author, literature citation, type citation, e.g., *Beilschmiedia latifolia* (Nees) Sa. Nishida, Ann. Missouri Bot. Gard. 86: 680. 1999. *Hufelandia latifolia* Nees, Syst. Laur.: 674. 1836. TYPE: Peru. Locality not indicated, 1835 (fl.), *Matthew 1433* (holotype, E!; isotypes, BM!, E!, K!, LE not seen, OXF not seen).
☐ Synonyms based on different types are placed in separate paragraphs, each beginning with the basionym, followed by other combinations (if appropriate), and citation of the type.
☐ A Latin or English diagnosis for each new taxon is provided, immediately following the new taxon's name and type designation and immediately preceding the English or Spanish description of the new taxon. The *International Code of Nomenclature for Algae, Fungi and Plants* (Glossary) defines a diagnosis of a taxon as "a statement of that which in the opinion of its author distinguishes the taxon from other taxa." The journal's suggested style for the Latin diagnosis of a new species might include "Haec species . . . affinis [similis], sed ab ea [eo] . . . distinguitur [differ]," or in place of "Haec species" beginning with "Species nova" or equivalent wording. Suggested style for the English diagnosis of a new species might include "This [new] species is related [similar] to . . . , but is distinguished [differs] from it by . . ." or equivalent wording. Reference to diagnostic characters elsewhere in the text (abstract, discussion, key, etc.) is not acceptable in place of the formal diagnosis.
☐ For species with infraspecific taxa: Description and discussion are composite (incorporating all infraspecific taxa) and parallel with other species descriptions. Descriptions of infraspecific taxa are parallel with one another (in the same species). All synonyms are listed under the appropriate infraspecific taxon.
☐ Descriptions: Descriptions are parallel, within a given rank. All measurements are metric. Hyphens are used for parenthetical extremes: "peduncle (8.2–) 14.3–28.0(–31.9) cm long," unless intermediate values are not expected: ovary with (2)4(6) locules. Length × width are given in the following manner: lamina 36.4–82.8 × 9.1–16.8 cm.
☐ When relevant, nomina nuda, misapplied names, and superfluous names are included in the discussion following the description, but are not part of the formal synonymy.

7. Citation of Types

☐ Exclamation points are used for specimens examined, and types not seen are indicated as such (e.g., MO!, US not seen).
☐ Lectotype designations are included together with an indication of where they were designated [author, year, page number, and herbarium of deposition; e.g., *C. J. W. Schiede 159* (lectotype, designated by Stevens [2000: 256], P!; isotypes. . .)]. This reference is listed in the Literature Cited. If the author of the paper submitted is making the lectotypification, the phrase "designated here" is used.

8. Tables

☐ Create tables using the Microsoft Word "Table" feature.
☐ Tables are neat, double-spaced, and clearly presented.
☐ Captions are typed double-spaced as paragraphs at the tops of the tables.
☐ Each table starts on a separate page.

9. Abbreviations

☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.
☐ When dates are given as part of collection information, three-letter month abbreviations are used, except for months with four letters, which are spelled out in full.
☐ States are not abbreviated, and cities are spelled out. [St., as in St. Louis, is acceptable.]
☐ Periodicals are abbreviated according to *B-P-H* (*Botanico-Periodicum-Huntianum*) and to *B-P-H/S* (*Botanico-Periodicum-Huntianum/Supplementum*).
☐ Authors' names are abbreviated according to Brummit & Powell's *Authors of Plant Names*.
☐ Book titles are abbreviated according to *Taxonomic Literature, edition 2*, but with initial letters capitalized. Book titles are spelled out in the Literature Cited.
☐ If an item does not appear in *B-P-H* or *TL-2*, or if these references are not available, its title is fully spelled out.
☐ Herbaria are abbreviated according to the most recent edition of *Index Herbariorum*.
☐ Abbreviated forms are not used for references in the text, except when citing the names of plants. If it is necessary to cite a particular page in the text, the form Smith (1998: 12) is used.

10. Specimens Examined

☐ If many specimens were examined, those cited in the text are limited to ca. 12 manuscript pages.
☐ If there are a large number, an index to specimens examined is placed at the end of the paper, following the Literature Cited. It is arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text. Names (including initial(s)) of first and second collector are provided, "et al." if three or more.
☐ Specimens are cited in the text as follows: *Additional specimens examined* (or *Selected specimens examined*). MEXICO. **Oaxaca:** Sierra San Pedro Nolesco, Talea, 12°37′N, 85°14′W, 950–1100 m, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional but are omitted from longer lists.] Countries are run together in the same paragraph, e.g., COUNTRY A. **Major political division:** . . . COUNTRY B. **Major political division:** . . . Separate paragraphs are used for major continental regions within major political divisions.

11. Specimen Vouchers and Genetic Sequences

☐ If the paper presents original data, associated herbarium vouchers are cited. [Vouchers for seed and/or other collections should be included where pertinent. Dependent on the paper, reference to the original wild source may be required.] Vouchers are also cited from common names, and uses are taken from specimen labels.
☐ Herbarium vouchers state the collector and number, herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question.
☐ Nucleic acid or protein sequences corresponding to equal or greater than 50 nucleotides are entered into an appropriate data bank, e.g., GenBank/EMBL. The accession numbers are provided before publication. [Long sequences (exceeding two pages) will not be routinely published.]
☐ Data sequences and tree files should be provided in Nexus format or alternatively submitted to the TreeBASE web site (<www.treebase.org>).
☐ Author accepts responsibility for establishing the accuracy of information provided.

12. Keys

☐ Keys are clear and have been checked carefully for consistency with the descriptions. Leads of each couplet are parallel.
☐ Dichotomous keys are indented.
☐ Infraspecific taxa are keyed separately, not in species keys.
☐ Authorities are listed for every species appearing in a key.

13. Literature Cited

☐ The Literature Cited contains full citations of all references cited in the text.
☐ All entries in the Literature Cited are cited in the text.
☐ Spelling of author(s) name(s) and years of publication have been double-checked.
☐ All entries have been verified against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.
☐ Periodicals are listed as follows: Author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H/S*. Volume: pages. No parenthetical part numbers after volume numbers are given unless each part is paginated separately.
☐ For more than one author, this style is followed: Author's last name, initial(s), second author's initial(s), last name & third author's initial(s), last name.
☐ Books appear as follows: author's last name, initial(s). Year. Full Unabbreviated Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication.
☐ For an article within a larger work, this style is followed: Author(s). Year. Name of the article. Pp. 00–00 *in* Name of the editor(s), Full Title of Larger Work. Publisher, City of Publication.
☐ Citations of work "in prep.," unpublished theses and dissertations, and similar references to inaccessible sources have been eliminated or kept to a minimum. They are not necessarily included in the Literature Cited.

14. Illustrations

☐ Electronic figures are labeled with the first author's last name, the first four letters of the taxon, and "...Figure1.tif", "...Figure2.tif", etc. The file extension clearly indicates what type of file it is.
☐ Scale bars appear on illustrations, photographs, and maps.
☐ Magnifications/reductions are not indicated in captions.
☐ Electronic scans may be pre-sized to fit either column width (2-5/8 in. or ca. 68 mm) or full-page width (5-1/2 in. or ca. 140 mm). [Maximum size for printed illustrations is 5-1/2 × 8-1/4 in.]
☐ Figures are numbered in Arabic numerals in the order of their citation in the text. Parts of figures are labeled with capital letters.
☐ Text in figures is in Times New Roman.
☐ Photographs are prepared according to the printer's requirements. [See Guide to Digital Art, Allen Press through the Publication Submission link on the opening page of <http://www.mbgpress.info/>.]
☐ Figures are grouped into composite plates when possible; edges of photographs are abutted.
☐ Edges of figures are squared.
☐ Maps include reference to latitude and longitude and are bounded by a fine border.
☐ Scanning electron micrographs are free of conspicuous charging.
☐ Axes on graphs are all labeled.
☐ Captions provide all explanatory text. Captions are separate from other text, one paragraph for each group of figures, and following the style in current issues of the *Annals*.
☐ Symbols on maps are legible, and reduction has been taken into consideration.

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Cover illustration. *Corymbia citriodora* trunk and canopy, Santa Barbara, California, U.S.A.